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CONTENTS

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THE ECOLOGY OF THE MERRIAM KANGAROO RAT (*DIPODOMYS MERRIAMI* MEARNS) ON THE GRAZING LANDS OF SOUTHERN ARIZONA

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INTRODUCTION

The Merriam kangaroo rat, *Dipodomys merriami* Mearns, a small rodent of the family Heteromyidae, inhabits the creosote-bush type and some desert shrub-grasslands of Arizona, California, Nevada, New Mexico, Texas, and Mexico. Much of this area is rangeland which is used primarily for the grazing of livestock. Because Merriam kangaroo rats subsist on and distribute the seeds of important range plants and also disturb the soil by burrowing activities, ecological knowledge is basic to formulating a program for the maintenance and use of these lands.

Between the lower desert lands, of little economic importance for grazing, and the higher, better grassed areas, the presence of Merriam kangaroo rats as well as other rodents is most important. In this transition zone, both animal and plant populations are delicately balanced. These lands yield an economic return from grazing domestic livestock. To maintain and improve this use requires an understanding of all environmental factors involved, both physical and biotic. The present analysis concentrates upon major limiting factors of the environment and presents a preliminary evaluation which it is hoped will make possible a sound economic attitude toward the Merriam kangaroo rat.

Many persons made this contribution possible. Some of the work was completed while the author was Assistant Range Ecologist in the Arizona Agricultural Experiment Station under the direction of P. S. Burgess. Raymond Price and Matt Culley of the Rocky Mountain Forest and Range Experiment Station, U. S. Forest Service, permitted use of the Santa Rita Experimental Range. R. A. Darrow of the Department of Botany and Range Ecology at the University of Arizona, helped identify plant material, and H. S. Haskell spent many hours afield assisting in the collection of data. A. Starker Leopold, O. P. Pearson, H. F. Heady and A. W Sampson, of the University of California, reviewed the manuscript, as did D. Brandt of Humboldt State College and Henry Anderson of the California Forest and Range Experiment Station.

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STUDY AREA

Nearly all work was conducted on the Santa Rita Experimental Range about 30 mi south of Tucson, Arizona. This Range extends from the typical creosote desert at an elevation of 3000 ft with annual rainfall of 9-10 in, to the oak-woodland at 4500 ft elevation with rainfall of 18-20 in. A wide variety of vegetational conditions resulting from controlled grazing by cattle since 1915 exist on the Experimental Range. Climatic, soil, vegetational, and wildlife records, some of which extend back to 1903, also provide an excellent background for the interpretation of results. Hence, the Experimental Range

is ideal for investigative work, since it provides fundamental basic data and a wide selection of vegetational conditions within the altitudinal distribution of Merriam kangaroo rats.

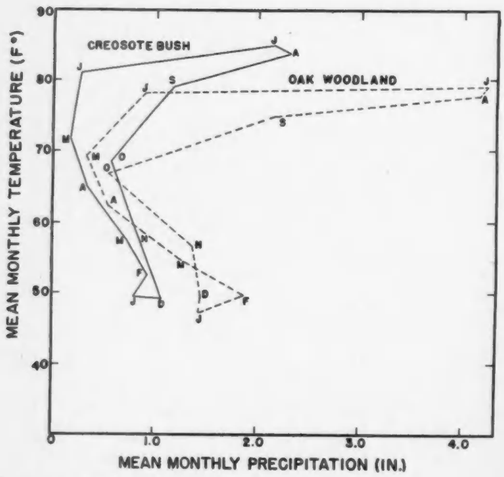

FIG. 1. Hythergraph for vegetative types at the upper (oak-woodland) and lower (creosote-bush) elevational limits of the Santa Rita Experimental Range.

The climate of the Santa Rita Experimental Range is representative of much of the habitat occupied by Merriam rats. The relation between temperature and precipitation is illustrated by hythergraphs (Fig. 1) bracketing the limits of the altitudinal distribution of this rodent in south-central Arizona. The two graphs for upper and lower limits of the Experimental Range are similar in form to those given by Smith (1940) for the entire desert grassland type. For the altitudinal limits of the desert grassland, average monthly precipitation varies from a low of 0.19 in in May to a high of 4.22 in in August. Mean monthly temperatures reach a low of 47°F in January, and rise to a high of about 85°F in July.

The desert grassland climate may be characterized in general by high rainfall and temperature in the summer, low rainfall and intermediate temperatures during the fall and spring, and low temperatures and intermediate rainfall during the winter. Average winter temperatures are high enough to permit growth of plants adapted to growing at low temperatures when rainfall is favorable. Hence, the climate permits growth of two groups of plants. One group matures during the late winter and early spring, the other during the summer. Amount of rainfall during either period limits the luxuriance of plant growth.

The oak-woodland vegetation at the higher elevations is well described by Nichol (1952), as is the creosote-bush or Sonoran desert type at the lower elevations by Shreve (1951). The intermediate or desert grassland areas (Fig. 2) have been described in terms of the three elevational units (Canfield 1948).

FIG. 2. The vegetation on the Santa Rita Experimental Range, which is fairly representative of the desert grassland type, varies considerably with elevation.
Top. At the higher elevations perennial grass is relatively abundant, and cacti and shrubs are rare.
Middle. At intermediate elevations shrubs and cacti are usually abundant, and perennial grass densities are lower.
Bottom. Below 3,000 ft elevation, shrubs are dominant, annual plants abundant, and perennial grasses rare.

FACTORS AFFECTING DISTRIBUTION

Geographic Range. The Merriam kangaroo rat is confined geographically to the southwestern United States, Baja California, and to northern states of Mexico (Fig. 3). In general, the range coincides (except for Nevada) with the distribution of creosote-bush and is characterized by low rainfall and humidity, high summer temperatures and evaporation rates, and poorly developed sandy or sandy loam soils.

Altitudinal Distribution. Merriam rats occur altitudinally from below sea level to about 4500 ft elevation. To gain a further appreciation of how numbers of animals vary with elevation and the factors that

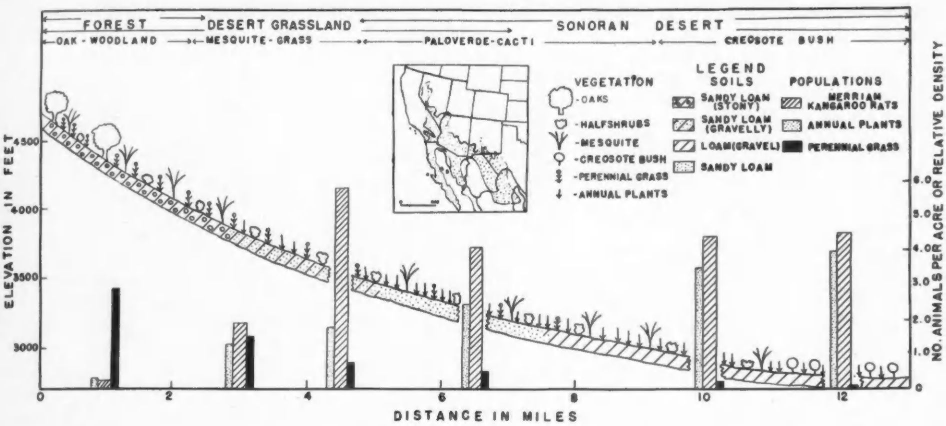

FIG. 3. Relation of soil, vegetation, and numbers of Merriam kangaroo rats to elevation on the Santa Rita Experimental Range. Inset: Geographical Range.

affect distribution, an altitudinal census was conducted on the Santa Rita Experimental Range in the fall of 1951. Snap-trap lines were located at 1-mi intervals in replication over a distance of 9 mi from the oak-woodland at 5500 ft to the creosote-bush at 2500 ft. The census technique, described on page 115, gave number of animals per acre. At each trapping site vegetation conditions were evaluated, and soil series (Youngs *et al.* 1936) and elevations were noted.

Numbers of animals vary considerably with elevation on the Santa Rita Experimental Range (Fig. 3). Above 4000 ft, Merriam rats were uncommon, averaging about 0.3 animals/acre in 1951. At 3500 ft, they reached their greatest abundance of about 6 animals/acre. At some 3200 ft, populations leveled off to a fairly constant number (about 4.5 animals/acre) which held well out into the creosote-bush type at the lowest elevations.

Controlling Factors. Within the general range of the Merriam rat several environmental factors have a controlling influence on local distribution and abundance. The most important of these factors are soil, kind and amount of precipitation, and winter temperatures.

Soil. The majority of soils occupied by Merriam rats are alluvial and poorly developed. Animals have weak forelegs. As a result, they are poor diggers, and their burrows are shallow and of simple construction. Huey (1942) noted that the species avoids rocky situations. This same author (Huey 1951) observed that these rodents cannot burrow into very hard soil and that the highest numbers are attained where the soil is loose and sandy. Hardy (1945) found in the vicinity of St. George, Utah, that Merriam kangaroo rats preferred fine soils, that a sulphate crust inhibited digging activities, but that shallow soils underlain by hardpan afforded a satisfactory habitat.

Soil characteristics vary widely on the Santa Rita Experimental Range. Trapping records indicate no relation between soil series and the abundance of these rats. Texture of soil, however, does have an effect. Heavy clay soils, and those having considerable stony outcrop or gravel composition are avoided.

When soils of the Experimental Range were divided into sandy loam and coarse sandy loam texture groups, significant differences in numbers of animals were apparent. The sandy loam soils averaged 7.6 animals/acre, and the coarse sandy loam soils 5.9 animals/acre. The difference is statistically significant. The sandy loam soils are not too heavy to discourage digging, neither are they so light as to allow tunnel cave-ins that occur in coarse sandy loam soils.

Precipitation. Kind, amount, and distribution of precipitation directly or indirectly affect the distribution of the Merriam rat. The species is active throughout the year, apparently does not store food in its burrows, and is dependent upon a plentiful seed crop for a food supply (Vorhies & Taylor 1922). Thus, a snow cover definitely places the animal at a disadvantage, since not only is the food supply covered, but the animal is discouraged from traveling in search of food. Except for Nevada, the northern distribution of this animal is confined to the 5-10 in snowfall line (U. S. Dept. Agric. Yearbook 1941).

The eastern and western limits of the species in the United States seem to be related to the amount and distribution of moisture as these interact with soil and plant cover. Distribution is confined almost entirely to regions receiving less than 10 in of annual rainfall.

Temperature and Humidity. Both high and low temperatures can be unfavorable to the existence of Merriam kangaroo rats. Their zone of thermal neutrality lies somewhere between 87.8°F and 93.2°F. Body temperatures below 72°F or above 86°F produce ill effects. These animals have relatively little ability to regulate heat. Above the zone of thermal neutrality, body temperatures tend to vary with those of the environment (Dawson 1955).

Individuals kept in captivity succumb to air temperatures that exceed 100°F or drop below a minimum of 45°F (Schmidt-Nielsen & Schmidt-Nielsen 1950). The isotherm of 30°F for average January temperatures corresponds in general with the northern limits of distribution of the species in the United States (U. S. Dept. Agric. Yearbook 1941). Freezing temperatures for any extended period, especially those sufficient to freeze the soil to any depth, are detrimental to existence.

The unfavorable effects of high temperatures are avoided by underground retreat during the daytime. Relative humidity of burrows in the early summer ranges from 30 to 50% and air temperatures range from 75° to 88°F. Comparable relative humidities of the night atmosphere are from 15 to 40%, and temperatures about 60°-75°F. Thus, protection of the burrow affords just enough shelter to permit these animals to exist under arid desert conditions (Schmidt-Nielsen & Schmidt-Neilsen 1953).

Vegetation. On the Experimental Range, an increase in elevation is associated with a decrease in temperature and higher precipitation. However, soils are shallower and more parent material is evident in the form of stone and gravel at the higher elevations. Density of perennial grass increases with higher precipitation, and largely replaces the annual grasses found abundantly at lower elevations. Merriam kangaroo rats seem to prefer areas occupied by annual grasses and a scattering of woody plants.

For any given elevation, or vegetation type, animal numbers decrease with an increase in the abundance of perennial grass. These latter plants create an unfavorable environment by interfering with ease of travel and escape from predators (Reynolds 1950). Thus, the increase in perennial grass under conditions of greater precipitation discourages Merriam kangaroo rats, in addition to the direct effect that climate has upon animals at the higher elevations.

Water. Experimental evidence indicates that availability of free water has little effect on distribution. Merriam kangaroo rats can exist entirely upon metabolic water (Schmidt-Neilsen *et al.* 1948); individuals have been kept alive on dry barley for long periods without decreasing their total water content. These animals conserve water by every possible means. They use little water for heat regulation, excrete a highly concentrated urine (Schmidt-Nielsen 1952), have a low evaporative loss from the lungs, and have the ability to decrease the ventilation of the lungs. Considering the nocturnal habit of this species, there is every reason to believe that there is a balance in favor of water gain by metabolism and that this source is sufficient to meet the needs of the animal (Schmidt-Nielsen & Schmidt-Nielsen 1949).

In summary, a light textured soil that is favorable to burrowing is an important factor limiting the range of Merriam kangaroo rats. Within the range of favorable soil, climatic factors become increasingly important. Since the animals are active throughout the year, rely on a food supply on the surface of the ground, and construct very shallow burrows, a blanket of snow, high rainfall, or low temperatures are detrimental to existence. Moreover, density of perennial grass which increases with elevation or precipitation progressively discourages high populations.

LIFE HISTORY

Several life history details are basic to an ecological evaluation of any animal species. Accordingly, observations were made on several life history details for the Merriam rat such as reproduction, breeding, and behavior of mature animals. A fuller consideration of life history details will be published elsewhere.

Young are born hairless and are blind for about two weeks. Animals crawl for about one week after birth; their hind legs are fully functional at the end of two weeks. Young animals will take solid food (rolled barley) by the 11th day after birth although supplementing their diet by nursing until about 3 wks of age. The hind foot reaches full development at 6 wks and tail at 10 wks, whereas full body growth continues slowly until an age of about 5 mos. The youngest animals captured in the field were about 3-4 wks old, some 1-2 wks after being weaned from the mother.

Merriam kangaroo rats breed before reaching full maturity. Males with swollen testes and pregnant females were captured at about 75% of adult weight for the season of the year. Males with scrotal testes on the Experimental Range varied from a low of 4% of the population in the winter to a high of 97% during the summer. Pregnancies were first noted in March, peaked during May and again in September, and were not observed during the winter months of November through February. Number of embryos per female averaged 2.02 (1-3).

Animals were observed to be strictly nocturnal in habit. Peaks of activity do, however, occur. One peak is reached about 2.5 hrs after sunset, and the other about 2.5 hrs before sunrise. Seasonally, there was no suggestion of hibernation or estivation.

Animals have fairly small home ranges. On the average, adult males occupied 0.466 acres; adult females, 0.373 acres; and immature animals irrespective of sex or age, 0.243 acres. During the breeding season, females appear to occupy exclusive territories, whereas home ranges of males overlap those of females and other males. Immature animals tend to occupy areas not occupied by adults.

POPULATION DYNAMICS

The line transect principle of sampling vegetation (Canfield 1941) was adapted to sampling populations of Merriam rats. The transects consisted of lines of 10 traps spaced 45 ft apart and trapped for three successive nights. Snap-trap lines correlated well with snap-trap quadrats, which in turn compared favorably with live-trap quadrats. By the use of border corrections (Dice 1938), the data from snap-trap

lines were expressed in animal numbers/acre. Lines were offset at mechanical intervals along roadways for randomization. Lines falling in rocky areas or sites otherwise uninhabitable by Merriam rats were not sampled. Sampling accuracy was set within 10% of the population mean with a probability of two chances out of three. About 12-15 lines were ordinarily required to meet this accuracy. The use of the snap-trap, line-transect technique greatly facilitated the study of Merriam rat populations. The small number of traps per sampling unit greatly reduced labor and made possible more adequate sampling of larger areas.

Variation in Numbers

Numbers of Merriam kangaroo rats vary widely with season of the year, and from one year to the next, as shown by seasonal changes recorded on the Santa Rita Experimental Range in 1946, and by yearly differences recorded for the period 1941-53. No permanency of population numbers or composition was suggested with the exception of sex ratios which showed little variation. Death losses, pressures of increased numbers of young, food changes, and catastrophes such as prolonged drought and floods, were continually altering population numbers and composition within the sample area of about 30,000 acres.

In March 1946 the population was composed entirely of adult or subadult animals at a level of about 4 animals/acre. From April until July immature animals accounted for a significant increase in the population. The population high of 5.6 animals/acre was reached in July. At this time the population was composed of 66% mature and 34% immature animals.

Numbers of Merriam kangaroo rats on the Santa Rita Experimental Range have varied from a low of 1.4 animals/acre in the winter of 1946 (Fig. 4) to a high of 7.0/acre in the winter of 1950. No predictable cyclic changes are apparent. Numbers change suddenly from year to year. Similar striking fluctuations have been noted in populations of *D. heermanni* in southern California (Horn & Fitch 1942).

Modifying Factors

Climate and Food Supply. Numbers of Merriam kangaroo rats are not well correlated with grass production or with annual precipitation (Fig. 4). However, some of the direct and indirect effects of rainfall upon numbers of those animals are explainable. For example, during favorable winters and springs considerable annual herbaceous growth is produced which makes available a bountiful food supply of seeds. Summer rains have a similar effect. If rains are of such kind and amount as to increase seed production, without actually drowning the animals, population survival is favored.

An example of the favorable effect of well distributed rainfall can be found in several different years. The spring of 1941 was exceptional, producing more spring annuals than had occurred for 10 years. In terms of rat numbers, there was a carry-over effect into the winter of 1942, resulting in a high winter population. A similar occurrence in 1952 resulted in a large population of rats during the winter of 1953. In 1950, spring growth was poor, but the summer rains were gentle and came almost entirely during the month of July. As a result, an excellent seed crop was produced. Merriam kangaroo rats responded to these favorable conditions by producing a high winter population.

Heavy summer precipitation can have a deleterious effect. Also, if enough of the winter precipitation falls as snow, a population of rats may be severely reduced. Between 1942 and 1943 populations dropped from 5.7 to 2.1 animals/acre. A comparable loss occurred between 1945 and 1946. Heavy downpours, such as occurred during the early fall of 1946, quickly exceed the infiltration capacity of the soil and run off the surface in large amounts. Any burrow on low ground suffers inundation with the resultant drowning of many animals. Similar reductions of Tulare kangaroo rats as a result of heavy storms have been observed by Fitch (1948). The catastrophe of flood is emphasized by Grinnell (1939) as the dominating factor upsetting population stability of small xerophilous rodents.

In summary, the most favorable rainfall pattern for high winter populations of Merriam kangaroo rats is good spring precipitation, which produces an abundance of annual growth, followed by mild summer precipitation without torrential downpours.

Predators. Owls, kit foxes, badgers, various snakes, and coyotes are known to prey upon Merriam kangaroo rats. Merriam rat skulls have been recovered in regurgitated pellets of the long-eared and great horned owls. Badgers have been observed digging out an occasional burrow, but they seem to prefer bannertail dens, possibly because nearly every active bannertail den yields an animal, while four or five Merriam dens must be excavated before an animal is found.

Predation seems to be a relatively unimportant factor limiting Merriam kangaroo rat numbers. Predators must be highly adapted to survive. Hence, most of them have a highly varied diet within which are kangaroo rats.

ASSOCIATED RABBITS AND RODENTS

Rabbits. These animals are common on the Santa Rita Experimental Range. Allen jackrabbits (*Lepus a. alleni*) reach populations of about 1 animal to every 5 acres; Arizona jackrabbits (*L. californicus eremicus*), about 1 animal to every 80 acres; and Arizona cottontails (*Sylvilagus auduboni arizonae*) about 1 animal per 14 acres (Culley 1939). Indirectly, lagomorphs compete with Merriam kangaroo rats for food. Competition does not, however, appear to be severe. The diet of rabbits is largely herbaceous material (Vorhies & Taylor 1933), whereas that of Merriam rats is seeds. Rabbits seldom eat so much herbaceous material as to interfere with seed production.

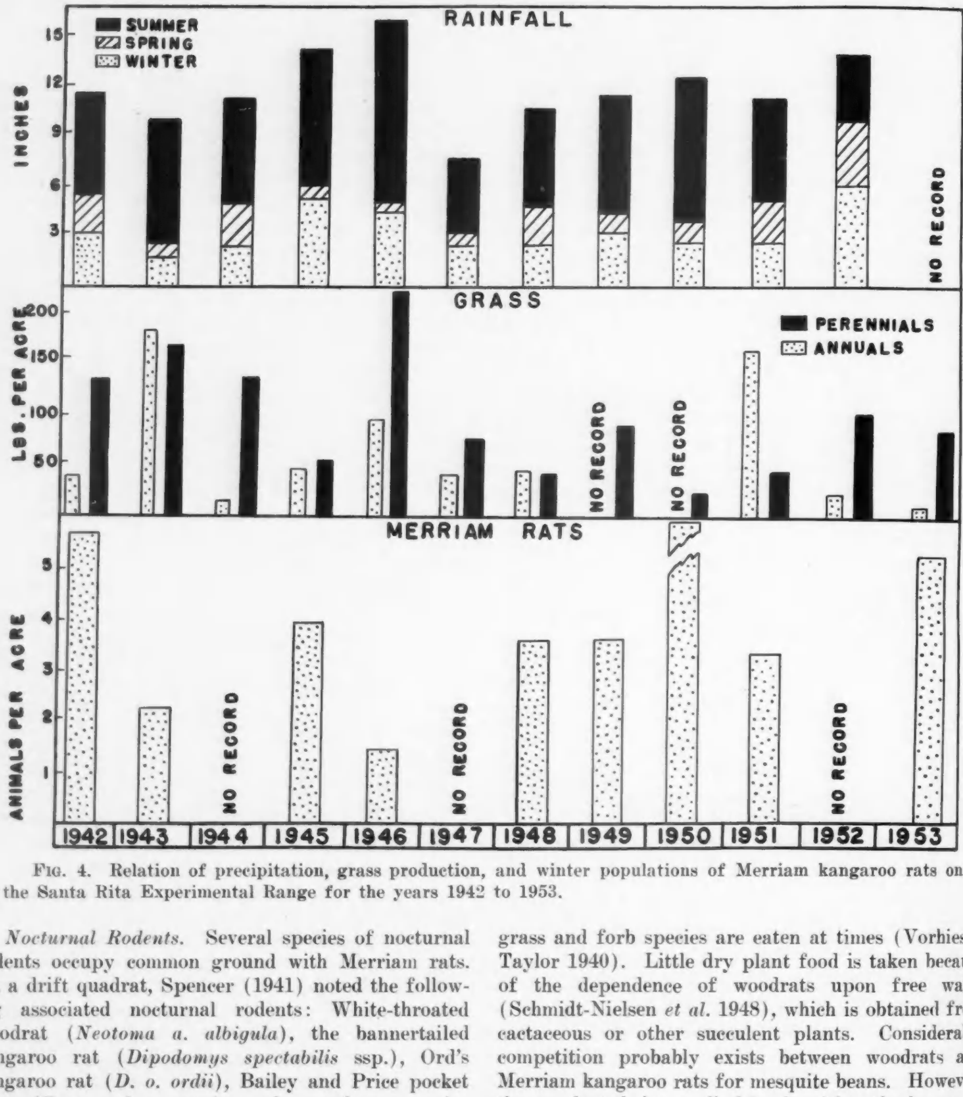

FIG. 4. Relation of precipitation, grass production, and winter populations of Merriam kangaroo rats on the Santa Rita Experimental Range for the years 1942 to 1953.

Nocturnal Rodents. Several species of nocturnal rodents occupy common ground with Merriam rats. On a drift quadrat, Spencer (1941) noted the following associated nocturnal rodents: White-throated woodrat (*Neotoma a. albigula*), the bannertailed kangaroo rat (*Dipodomys spectabilis* ssp.), Ord's kangaroo rat (*D. o. ordii*), Bailey and Price pocket mice (*Perognathus* spp.), and grasshopper mice (*Onychomys* spp.). Some other species of Dipodomys apparently do not exhibit this tolerance for other rodents. In California, Hawbecker (1944) found that *D. ingens* tolerated only *Citellus nelsoni*. The former is a diurnal and the latter a nocturnal species.

Bannertail kangaroo rats average about 1 animal/acre, whereas Merriam kangaroo rats exceed 3 animals/acre over a greater part of the Experimental Range. The major portion of the diet of bannertail kangaroo rats is herbaceous material (Vorhies & Taylor 1922), so there is little competition for food with Merriam kangaroo rats.

The white-throated woodrat nearly equals the bannertail kangaroo rat in abundance. The main foods of the woodrat are mesquite beans and cactus. Some grass and forb species are eaten at times (Vorhies & Taylor 1940). Little dry plant food is taken because of the dependence of woodrats upon free water (Schmidt-Nielsen *et al.* 1948), which is obtained from cactaceous or other succulent plants. Considerable competition probably exists between woodrats and Merriam kangaroo rats for mesquite beans. However, the woodrat, being a climber, furnishes the kangaroo rats with mesquite beans which would otherwise be unavailable. Woodrats cut mesquite pods when seeds are in the formative stage, and rats pick up many pods from the ground. Thus, woodrats assist kangaroo rats in obtaining food during a very critical period—June and July—when the spring seed supply is largely exhausted and summer herbaceous plants have not yet formed seeds.

The nocturnal rodent population on the Santa Rita Experimental Range in 1950 was composed of the Ord kangaroo rat; three species of pocket mice: Bailey (*P. b. baileyi*), Price (*P. penicillatus pricei*), and Baird (*P. f. flavus*); grasshopper mice; and two species of white-footed mice (*Peromyscus e. eremicus* and *P. maniculatus sonoriensis*). Relative numbers of

these species change greatly from year to year. Between 1946 and 1950, numbers of animals/acre averaged as follows: Merriam kangaroo rats, 5.0; Bailey pocket mice, 0.3; Price pocket mice, 0.7, and grasshopper mice, 0.4. Baird pocket mice, Ord kangaroo rats, and white-footed mice were uncommon on the trapping area.

Competition between Ord and Merriam kangaroo rats is reduced by differences in soil preferences. The former are confined to coarse sandy soils along ravines and arroyos, whereas the latter are found on sands and clay loams of the mesas. Seed diets of the two animals are similar. White-footed mice prefer green food material and obtain part of their food supply by climbing shrubs and trees. This reduces competition for food with Merriam kangaroo rats. Price and Bailey pocket mice exist largely on seeds, but seem to prefer slightly larger seeds than Merriam kangaroo rats. Also, pocket mice prefer a heavy protective cover of grass that is avoided by Merriam kangaroo rats (Reynolds & Haskell 1949).

Diurnal Rodents. Two species of ground squirrels are found in the vegetational type occupied by Merriam rats—the roundtailed ground squirrel (*Citellus tereticaudus neglectus*), and the Harris ground squirrel (*C. h. harrisi*). The roundtailed ground squirrel eats mostly green vegetation. The Harris ground squirrel subsists largely upon green forbs during the growing season, and fruits and seeds of shrubs and cacti at other periods (Howell 1938). Together, these squirrels seldom exceed an abundance of one animal to every two acres (Culley 1939). They do not seem to compete seriously with Merriam kangaroo rats for food.

FEEDING HABITS

FOOD CONSUMPTION

Laboratory feeding trials were used to estimate the amount of food required by the Merriam rat. The amount of rolled barley necessary just to maintain body weight was used as the basis for estimating maintenance requirements. All animals were kept in wire cages small enough to restrict movement to a minimum consistent with general good health. Animals were given a feeding tray; and were provided with a shelter to occupy during the day. Feedings were made daily to counteract the storing or hoarding tendency, and slightly more than enough rolled barley was offered at each feeding to maintain body weight. Measurements of amount of food material consumed and body weight changes were made weekly.

During the spring of 1942, 5 animals of each sex were maintained on a diet of rolled barley over a period of 10 wks. During the first few weeks prior to actual feeding trials, adjustments were made in amount of the ration to prevent individual animals from gaining or losing weight. Animals deviating more than 5% from initial live weight were not used in computing maintenance requirements.

There was no statistically significant difference in the amount of rolled barley eaten by different sexes (Table 1). However, individual animals within each sex required different amounts of rolled barley for maintenance, and the difference between feeding periods was highly significant. Accordingly, the most accurate estimate of maintenance requirements that can be obtained for these trials is an average of all weeks and all animals. On this basis, the maintenance requirement of Merriam kangaroo rats for rolled barley is 4.9±0.1 g/day, which amounts to 12% of body weight. Total consumption of rolled barley for a year would amount to about 4 lbs/individual. In some years, Merriam kangaroo rats are sufficiently abundant to eat all large perennial grass seed produced. In a low rainfall year, such as 1948, less than 25 lbs/acre of seed of such perennial grasses as Plains bristlegrass (*Setaria macrostachya*), Arizona cottontop (*Trichachne californica*), and tanglehead (*Heteropogon contortus*) were measured on sample plots. Six or seven animals per acre are not uncommon and could thus consume all of this seed. In ordinary or above average years, however, there is sufficient seed to nourish rodents with enough additional for reproduction of desirable grasses.

TABLE 1. Analysis of variance of maintenance feeding trials with Merriam kangaroo rats on a ration of rolled barley.

Degree of Variation	Degrees of Freedom	Mean Squares	F	Significance
Replications	4	0.1970	1.647	N. S.
Periods (P)	1	7.5900	23.390	* *
Sex (S)	1	.3283	1.012	N. S.
Individuals (I)	4	4.8706	15.010	* *
P x S	1	.9507	2.930	N. S.
S x I	4	2.9277	9.022	* *
P x I	4	.6849	2.111	N. S.
Error	80	.3245	......	....

FOOD ITEMS COLLECTED

Food habits were studied largely by pouch analyses of animals captured in snap-traps in connection with population studies. The nocturnal habits of Merriam kangaroo rats, the rapidity with which they move, and the minuteness of the material which they eat, largely precluded direct observation. Stomach and scat analyses were attempted but proved too difficult, because food material was masticated too minutely.

From November, 1942, to September, 1943, and from March through November, 1946, 1,001 pouch contents were collected and analyzed. This series of pouch collections is fairly representative of the many kinds of food material eaten by Merriam kangaroo rats on the Santa Rita Experimental Range.

Seeds make up the majority of plant items found in pouch contents (Table 2). Ninety-five percent of the identified items were seeds while other vegetative parts (leaves, stems, and roots) constituted the remainder. Grass seeds were most abundant, forbs were

TABLE 2. Percent frequency of occurrence of seeds compared with other vegetative parts (leaves, stems, and roots) in pouch contents of Merriam rats for the months of the year.

Month	Percent								Number	
	Seeds				Other vegetative parts					
	Grasses	Forbs	Shrubs	Total	Grasses	Forbs	Shrubs	Total	Pouches	Frequencies
January	32	33	24	89	3	5	3	11	72	149
February	30	35	26	91	3	1	5	9	46	66
March	49	32	12	92	0	4	4	8	88	171
April	43	37	11	91	1	7	1	9	54	95
May	52	29	8	88	2	9	1	12	79	140
June	49	29	16	93	2	4	1	7	83	206
July	38	29	37	97	1	1	1	3	76	128
August	34	51	10	96	2	2	0	4	71	105
September	39	55	4	97	1	2	0	3	118	243
October	81	13	2	97	1	2	0	3	109	202
November	55	28	6	99	0	1	0	1	139	304
December	47	40	8	96	1	3	1	4	66	141
Total	49	33	12	95	1	3	1	5	1,001	1,950

second, and shrubs were third. Among other plant parts, forbs occurred most frequently.

Seeds of over 60 species of plants, representing 27 families, were recovered in pouch contents (Table 3). No plant family was particularly favored. Characteristics of individual species of plants seem to influence selection more than any taxonomic family relation.

Several species of seeds were preferred. Annual threeawn *(Aristida adscensionis)*, with 32.4% occurrence in cheek pouches, led all species. The perennial threeawns *(A. hamulosa, A. ternipes,* and *A. divaricata)*, with 20.1%, and annual grama *(Bouteloua aristidoides)*, 19.3%, were also important. A group of species which ranged from 8 to 12% occurrence in pouches included: *Boerhaavia torreyana*, 11.7%; *Sida diffusa*, 10.3%; *Prosopis juliflora*, 9.4%; and *Evolvulus arizonicus*, 8.3%. *Aristida glabrata* and *Lotus humistratus*, from about 6.0 to 7.0% occurrence, were next in order of selection. Among other species of significant occurrence were: *Opuntia engelmanni*, 4.9%; *Euphorbia* spp., 4.4%; *Pectocarya recurvata*, 4.1%; *Trichachne californica*, 3.8%; *Opuntia* spp., 3.0%; *Panicum arizonicum*, 3.0%; and *Bouteloua rothrocki*, 2.9%.

SEASONAL PREFERENCES

Percentage occurrence of seeds in cheek pouches varied considerably with months (Table 3). Collections for the period March-May and July-September represent mostly material harvested directly from plants, or taken immediately after seed has fallen to the ground. Pouch contents of other months also have some material collected from the surface of the ground, but probably the majority is obtained from surface caches which are reopened during periods of seed scarcity.

During the spring-seeding period, the annuals, *Festuca octoflora* and *Gilia filifolia*, were used heavily. Other spring annuals, such as *Aristida adscensionis* and *Pectocarya recurvata*, received highest use during the spring seeding period, although seeds of these species were recovered in pouches at other periods of the year.

Perennial grasses, other than the *Aristida* spp., were used almost exclusively in the late summer after seed maturation. Those summer-growing species that were used throughout the year, but which received heaviest use during the summer, included *Aristida glabrata*, other *Aristida* spp., *Boerhaavia torreyana, B. caribea, Panicum arizonicum, P. hirticaule, Prosopis juliflora,* and *Solanum elaeagnifolium*.

Plant species used throughout the year without respect to their seeding habits included *Bouteloua aristidoides, Euphorbia* spp., *Evolvulus arizonicus, Sida diffusa, Opuntia* spp., and *Echinocactus wislizeni*. Plants in this group, other than cactus, have several characteristics in common which influence their selection throughout the year. All were abundant and are low-growing. Thus, fruits can be harvested directly from the plants. Moreover, some of them maintain their fruits for long periods of time after maturation of the seeds. All species of this group, except *Bouteloua aristidoides*, will, during favorable springs, produce flowers and a seed crop both in the spring and in the summer. Cacti, as a group, have a tendency to retain their fruits, dropping them intermittently, thus making seeds available over a long period of time.

Other species occurred most abundantly in pouches during the periods when seed is not produced. Examples of this group include summer annuals, such as *Mollugo verticillata*, which receives heaviest use during the spring, and spring annuals, such as *Lotus humistratus*, which appeared most frequently in the pouches during the winter.

ANNUAL VARIATIONS

Amount and kind of seed collected by Merriam kangaroo rats were not constant from year to year. Wide differences in species of seeds in pouch contents occurred between 1942 and 1946 (Table 3). Notable

TABLE 3. Percent occurrence of seeds by species in cheek pouches by months for all trapping years combined.

Plant	Month												Years		
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	All	1942	1946
Grasses, annual															
Aristida adscensionis	10.0	7.5	13.6	22.1	24.4	20.3	10.2	—	—	—	—	—	32.4	18.7	19.1
Bouteloua aristidoides	7.1	10.1	11.9	8.4	12.8	11.4	10.9	—	10.3	9.4	10.5	9.7	19.3	13.0	8.3
Festuca octoflora	—	—	1.1	4.2	1.4	2.8	2.3	—	—	—	—	—	1.7	0.7	—
Panicum arizonicum	0.7	—	1.1	1.1	0.7	—	—	12.4	2.1	2.5	0.3	0.7	3.0	3.5	2.2
Panicum hirticaule	2.0	—	—	1.0	0.7	0.5	0.8	2.8	0.4	0.5	1.3	0.7	1.7	0.9	1.4
Grasses, perennial															
Aristida glabrata	0.7	1.5	1.7	3.2	5.0	4.3	1.6	—	9.1	6.0	3.3	—	7.0	6.9	3.9
Aristida, other	9.5	9.0	13.6	2.1	6.5	6.2	2.3	—	3.3	25.7	18.7	9.0	20.1	19.6	8.3
Bouteloua rothrocki	—	—	—	1.8	—	—	—	1.4	7.6	1.8	5.8	12.1	2.9	4.3	—
Heteropogon contortus	0.7	—	—	—	—	—	—	—	0.8	1.0	0.3	0.7	0.7	—	1.4
Setaria macrostachya	—	—	1.1	—	—	0.5	0.8	1.9	0.4	3.0	1.0	—	1.6	1.5	1.7
Trichachne californica	0.7	—	0.6	—	—	1.0	0.8	15.2	2.5	4.0	1.0	—	3.8	3.0	5.6
Forbs, annual															
Boerhaavia torreyana	0.7	—	1.1	2.1	2.9	2.8	1.5	28.5	23.0	2.0	2.9	0.7	11.7	15.6	8.1
Euphorbia spp.	—	—	3.4	2.1	2.9	4.3	1.6	1.0	1.2	1.5	4.6	—	4.4	2.6	3.1
Gilia filifolia	—	1.5	—	2.1	3.6	5.2	1.5	0.9	—	0.4	—	—	2.3	0.4	0.6
Lotus humistratus	8.2	10.1	1.1	—	—	—	0.8	0.9	3.7	1.0	2.0	15.9	6.3	3.7	0.6
Mollugo verticillata	—	—	5.1	1.1	—	—	1.6	1.0	0.4	—	—	—	1.4	0.2	0.8
Pectocarya recurvata	4.2	7.6	0.6	11.6	1.4	2.4	1.5	0.9	—	—	1.0	3.5	4.1	0.9	0.6
Forbs, perennial															
Boerhaavia caribea	—	—	—	2.1	3.6	—	1.6	1.9	2.5	—	0.3	2.1	2.1	2.0	0.6
Evolvulus arizonicus	3.4	—	5.7	7.4	2.9	1.0	3.9	3.8	9.5	3.0	4.6	2.1	8.3	8.0	4.2
Sida diffusa	3.3	3.0	5.1	1.1	6.4	4.2	5.5	6.7	8.2	2.5	5.9	7.6	10.3	7.2	6.7
Solanum elaeagnifolium	—	1.5	3.4	—	0.7	0.5	3.9	1.0	0.4	—	0.7	0.7	1.9	0.2	2.2
Shrubs															
Echinocactus wislizeni	0.7	1.5	0.6	—	1.4	0.5	—	—	—	—	1.0	1.4	1.1	0.7	—
Opuntia engelmanni	6.0	—	2.9	6.3	0.7	1.4	8.6	5.7	1.2	0.5	0.7	1.4	4.9	0.9	5.3
Opuntia spp. (cholla)	5.4	9.0	2.8	1.0	2.1	1.4	0.8	—	0.4	—	0.7	—	3.0	0.7	0.3
Prosopis juliflora	6.0	12.0	2.8	3.2	2.9	10.4	27.4	4.8	1.2	2.0	1.0	2.1	9.4	5.0	4.7
Unidentified	—	1.5	2.8	—	—	2.4	—	—	—	—	0.3	2.1	1.5	0.2	—
Number of Pouches	72	46	88	54	79	83	76	71	118	103	139	66	1001	461	360

was the appearance of *Festuca octoflora, Bouteloua rothrocki*, and *Echinocactus wislizeni*, in pouch collections in 1942 but not 1946; and *Heteropogon contortus* in 1946 but not 1942. *Echinocactus* and *Heteropogon* are fairly rare genera and the differences may be assigned to sampling error. *Festuca octoflora* and *Bouteloua rothrocki* are plant species which exhibit a marked response to differences in climatic conditions. The former, a spring annual, requires an abundance of spring moisture; and the latter, a summer semi-perennial, requires ample, well distributed rainfall during its growth period. The rainfall differences of 1942 and 1946 were great enough to account for variation in abundance of these plants.

Relative importance of plant species in pouch contents varied between 1942 and 1946. In 1942, both *Lotus humistratus* and *Pectocarya recurvata* were among the leading species, which again reflects the superior spring rainfall conditions of 1942, since both of these species are spring annuals. In 1946, conditions were more favorable for summer perennials, and *Opuntia engelmanni, Solanum elaeagnifolium* and *Heteropogon contortus*, all summer perennials, were among the leading species in that year. Significant differences also appeared among leading species that were common to the years 1942 and 1946. *Aristida* spp., *Boerhaavia torreyana*, and *Lotus humistratus* were all more abundant in cheek pouches in 1942 than in 1946. Yearly comparisons re-emphasize the conclusion that Merriam kangaroo rats are opportunistic in their feeding habits. Those plants which ranked high in selection were the ones that are fairly consistent seed producers.

FACTORS AFFECTING FOOD PREFERENCES

Amount of Seed. During 1946 a record was kept of numbers of plants, the seed of which was available for consumption by Merriam kangaroo rats, on several representative areas. Relative abundance of each species was expressed as a percentage of the total number of plants on the quadrat. Differences in numbers of seeds between plants of the same species are as great as those between species, so plant composition roughly represents relative seed abundance (Stevens 1932). Since there were wide differences in the percent abundance and collection of various seeds, these absolute differences were expressed on a relative basis, by dividing percent frequency of occurrence in cheek pouches into percentage composition of plants. The resulting figure is termed "preference rating."

A comparison of preference ratings showed preferred seeds to be: *Opuntia* sp. (pricklypear), *Setaria macrostachya, Prosopis juliflora, Heteropogon contortus*, and *Gilia filifolia* (Fig. 5). Species which occurred frequently in pouch contents because they were abundant and clearly not because they were preferred included *Bouteloua aristidoides* and *Boerhaavia* spp. Those plants intermediate between the above

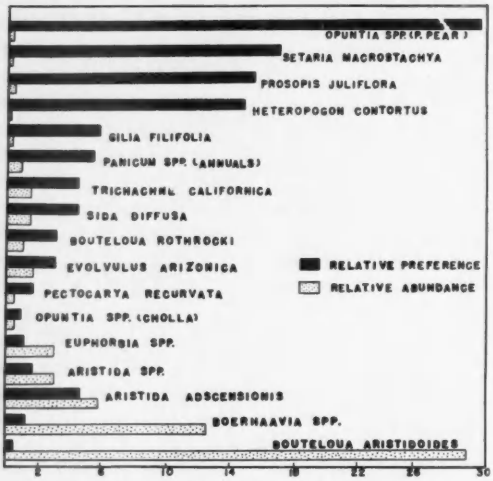

FIG. 5. A comparison of relative preference and abundance of plant species favored by Merriam kangaroo rats on the Santa Rita Experimental Range in 1946.

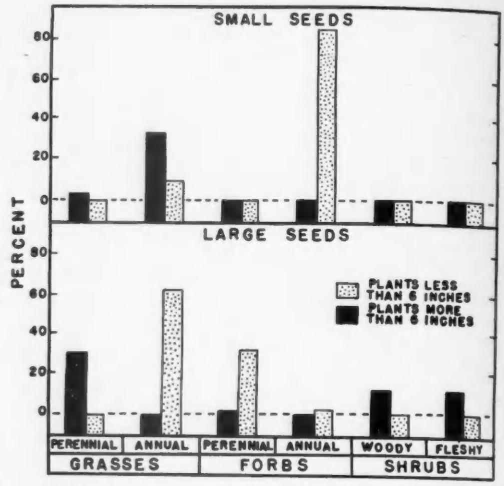

FIG. 6. Seed preferences of Merriam rats in relation to size of seed and stature of plant by classes of grasses, forbs, and shrubs.

two groups were selected almost in order of their abundance of occurrence.

Size of Seed. Plant material must be gathered with the forefeet to be placed in cheek pouches. Accordingly, pouch capacity sets a maximum size, and manual dexterity a minimum size, to seed which can be handled. No seeds too large for the pouch are known in the environment that the rat occupies. But many plants in the habitat of the rat produce seeds too small to be manipulated by the forefeet.

A significant regression was obtained when the preference rating of each species of seed taken in pouch collections was compared with number of seeds by unit weight for the plant species. Departures from the regression line suggested, however, that factors other than size of seed influenced seed preference. *Gilia filifolia,* with 5,040,000 seeds/lb; *Pectocarya recurvata,* with 1,561,000, and *Bouteloua rothrocki,* with 1,420,000, departed farthest from the regression. These small seeds were probably harvested as fruits rather than as individual seeds.

Stature of plants. The effect of size of seed upon preference interacts with stature of plants. Seeds collected by rats can be divided into three main groups—grasses, forbs, and shrubs; subdivided into annuals and perennials by these main groups; and then each subgroup can be expressed as percentages for different sizes of seed and statures of plant. Also, seeds can be divided into groups larger and smaller than 500,000 seeds/lb. Animals have difficulty in handling seeds smaller than this lower limit. Since Merriam kangaroo rats cannot reach higher than 6 in, this height was used as a stature division.

In general, small seeds are harvested from low growing plants, and large seeds from either tall or short plants (Fig. 6). Insignificant amounts of small seed are taken from tall plants, especially among perennial grasses. Low growing plants furnish the largest amounts of seed. Animals presumably harvest considerable seed directly, since it is easier to handle while still encased in fruits. Moreover, much less time would be expended in harvesting several seeds from a fruit than in searching for individual seeds on the ground.

Some seeds must be harvested as fruits, since the seeds are too small to permit individual handling. Seeds of such plants as *Mollugo verticillata, Talinum aurantiacum, Portulaca suffrutescens,* and *Bouteloua rothrocki* are collected in this manner.

Seeds of such shrubby species as *Prosopis juliflora* and *Opuntia* spp. must be harvested from the ground. Plants are 3-12 ft tall before seed is produced. Merriam kangaroo rats are not adapted for arboreal activities so that seed only becomes available when it falls to the ground. Most shrubs produce large seeds that are probably among the easiest for rats to recover.

STORAGE HABITS

Merriam kangaroo rats store seed in excess of immediate needs in small surface caches (Fig. 7). This adaptation is similar to that of several other species of the genus. Hawbecker (1940) observed that *D. venustus* stored seed from the mouth of the den out to distances of 168 ft. In captivity, *D. heermanni saxatilis* was noted to excavate small holes in the sand, to deposit seed, and to cover it by tamping in soil with the front feet (Dale 1939). The giant kangaroo rat uses unburied surface caches which resemble haystacks (Shaw 1934). These stacks may be 4 x 4 x 24 in. in size (Hawbecker 1944). Similarly, the Tulare kangaroo rat makes surface caches of a quart or more of seeds at the ends of surface runways (Horn & Fitch 1942). Pits, located in burrow chambers below ground, are used for food storage by *D. nitratoides exilis* (Culbertson 1946). Food storage

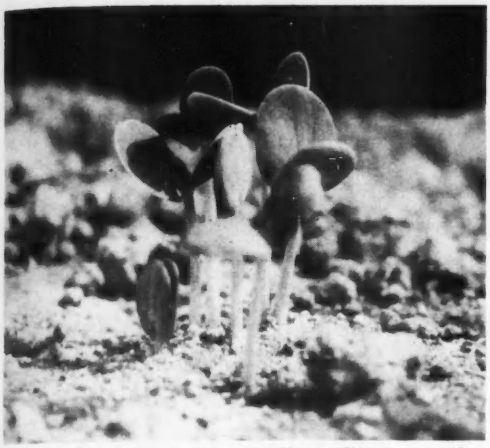

FIG. 7. A group of mesquite seedlings sprouting from a surface cache of seeds made by a Merriam kangaroo rat.

of *D. heermanni tularensis* (Tappe 1941), and *D. s. spectabilis* (Vorhies & Taylor 1922) consists of piles in the burrow chambers.

SEED STORAGE

During the summer of 1950 the seed caching habits of Merriam kangaroo rats were investigated. Three different sites on the Santa Rita Experimental Range were trapped with Spencer live traps radially located about a rolled barley central feeding station. Merriam kangaroo rats were marked and released, and other small nocturnal rodents were removed.

At the end of one week, on July 1 and 2, 210-250 seeds of mesquite were mixed with an equal amount of sudan grass and placed at each central feeding station. By July 4, all seeds had been removed. By July 10, the sudan and mesquite seeds had sprouted in response to favorable summer rains. The sprouting sudan, being different from all other native grass seedlings, served as a marker for mesquite seed planted by rats.

From 8 to 11 seed caches were discovered at each of the three trapping sites (Table 4). Seed was cached in random groups about the central feeding stations. On the average, mesquite seeds were found in about 24% of the caches. Combining all caches, 1.8 (0.5-2.8)% of the mesquite seed placed at the feeding stations was recovered.

Distances that seed was transported before deposition in caches varied from 2 to 105 ft. The average distance of transportation, considering all sites and caches was 46.8 ft. This is well within the average radius of home range (50-80 ft) determined by live-trapping.

SEED RECOVERY

The presence of numerous pits, about the size and depth of surface caches, scattered over the sites occupied by Merriam kangaroo rats suggests that caches are reopened when other sources of seed are

TABLE 4. Distance and number of mesquite seed caches made by Merriam kangaroo rats.

	STUDY AREAS			
	Site I	Site II	Site III	Average
Number of Merriam rats captured in one night (maximum)	4	8	8	6.7
Total other nocturnal rodents removed from site				
Bannertail rats	0	1	2	1.0
Pocket mice	0	0	1	0.3
Grasshopper mice	1	0	1	0.7
Woodrats	0	0	1	0.3
Total number of seed caches	10	8	11	9.7
Number seed caches containing mesquite	4	2	1	2.3
Percent seed caches containing mesquite	40	25	9	23.7
Average distance of seed transportation (ft.)	59	85	13	46.8
Range of distances of seed transportation (ft.)	28-90	73-105	2-31	2-105
Total number mesquite seeds offered	250	250	210	237
Number mesquite seeds recovered in caches	7	4	1	4.0
Percent mesquite seed recovered in caches	2.8	2.0	0.5	1.8

unavailable. To get an indication of the ability of rats to rediscover caches, a recovery experiment was conducted in the summer of 1946. Two animals, three sizes of seed, and three depths of planting were employed.

Animals were confined to artificial burrows, but allowed to roam freely over about 60 sq ft of soil enclosed by hardware cloth. Seeds of milo, rape, and bluegrass were planted in random locations at depths of 0.25, 0.5, and 1 in. in the enclosed area each evening and marked with greenhouse labeling stakes. Dummy caches were also made to determine whether marker stakes had any effect upon discovery of caches.

TABLE 5. Effect of depth of planting and size of seed upon discovery of seed caches by Merriam kangaroo rats.

Animal	Seed species	DEPTH OF PLANTING (inches)			
		0.25	0.50	1	Dummy
		(Pct.)	(Pct.)	(Pct.)	(Pct.)
I	Milo	87	100	62	25
	Rape	87	100	62	25
	Bluegrass	38	38	12	0
II	Milo	87	75	62	0
	Rape	100	100	62	0
	Bluegrass	100	100	75	0
Avg.	Milo	87	88	62	12
	Rape	94	100	62	12
	Bluegrass	70	70	44	0
	Average	83	85	56	8

For caches planted at 0.25 in, 83% were discovered; at 0.5 in, 85%; and at a depth of 1 in, only 56% (Table 5). The dummy caches indicated that labeling stakes had an unimportant effect upon discovery. This experiment suggests that most, but not necessarily all, seed caches are rediscovered.

Apparently smell is the important sense determin-

ing rediscovery of caches. Animals certainly had no *a priori* knowledge of caches. In this regard, the western fox squirrel *(Sciurus niger rufiventer)*, although using memory for general location, is believed to rely almost entirely upon sense of smell in the discovery of individual nuts of oak and hickory buried the previous fall (Cahalane 1942).

BURROW SYSTEMS

Merriam kangaroo rats spend fully 75% of their lives below ground. The burrow serves to ameliorate the hot, dry environment during the daylight hours, as a birthplace for young, and as a refuge from predators.

Burrows are neither conspicuous nor elaborate (Fig. 8). In contrast to the bannertail kangaroo rat, which constructs a conspicuous mound characterized by a labyrinth of storied tunnels (Vorhies & Taylor 1922), the Merriam kangaroo rat builds an inconspicuous, simple burrow which is usually under the protection of an overhanging shrub.

FIG. 8. An excavated main burrow system of a male Merriam rat showing the shallow, simple construction pattern. Openings are marked by wads of paper.

With regard to general location of burrow systems, Monson & Kessler (1940) have observed that these rodents tend to live in colonies composed of a half-dozen to several hundred dens. On the Santa Rita Experimental Range, burrows are characteristically located beneath shrubs. Of the total number of burrows counted on a 7.5-acre plot, 93% were located under the protection of tall shrubs, 3% were under half-shrubs, and only 4% were in the open with no overstory protection.

Mesquites were the favored location for burrows. Ninety-nine percent of the mesquites on the observation plot had a rat burrow beneath them. The remaining mesquite trees were understoried by bannertail rat burrows. Seventy-six percent of the catclaws *(Acacia greggi)*, and 50% of the desert hackberries *(Celtis pallida)* had Merriam kangaroo rat burrows beneath them. Other plants undermined by Merriam kangaroo rat burrows included: tall shrubs; cactus, whitethorn *(Acacia constricta)*, and wolfberry *(Lycium* sp.); halfshrubs, shortleaf baccharis *(Baccharis brachyphylla)* and burroweed.

EFFECT ON SOIL

Animals in their foraging, home-building, and other activities have both direct and indirect effects upon soil building and maintenance (Taylor 1935). Accumulation of animal parts, and waste material from houses, shelters, and nests locally enrich the soil. Digging of burrows brings sublayers of the soil to the surface, promotes water infiltration and retention, otherwise improves the mechanical properties, or leads to soil displacement. The known influence of the white-throated woodrat and bannertail rat on soil properties suggests strongly that burrowing animals on the Santa Rita Experimental Range indirectly affect plant production (Greene & Reynard 1932; Greene & Murphy 1932). Since the Merriam kangaroo rat is a burrowing rodent, some of the effects that this animal has upon physical and chemical soil properties were investigated.

SOIL DISTURBANCE

Natural Cultivation. Merriam kangaroo rats do not have a great influence upon soil cultivation, because the burrowing adaptation is not well developed. Den counts on a 7.5-acre sample plot in 1942 showed 23.5 burrows/acre. A similar plot counted in 1946 indicated 17.2 dens/acre.

Calculations suggest that a representative Merriam kangaroo rat population moves about 8 cu ft of soil/acre in the construction of a population burrow system. This figure was obtained as follows: Each main burrow averages 15 ft in length; one submain burrow, 10 ft; 2 escape burrows, 2.5 ft each. An average burrow is thus 7.5 ft. in length. Burrows are about 3 in in diameter. Hence, about 0.4 cu ft of soil is moved in the construction of the average burrow. With an average of about 20 burrows/acre, 8 cu ft of soil is displaced. This amounts to about 0.0036% of the soil habitat occupied by Merriam rats. Even if this amount of soil were moved annually and a new site selected each year, which is not the case, it would take more than 30,000 years to disturb completely the surface 6 in of soil.

Earthen Structures. Artificial soil structures are often constructed on grazing lands in such forms as contour furrows, percolation pits, and dams to promote infiltration of precipitation. Burrowing activities of Merriam kangaroo rats do not interfere with the effectiveness of these structures. In fact, tunneling and loosening the soil may benefit the structures by helping to keep the soil open and porous.

Large earthen dams or surface tanks are often used to trap surface runoff for use by cattle. Merriam kangaroo rat tunnels weaken these structures and may in some cases contribute to their destruction by opening seepageways and tunnels. In this regard, burrows of bannertail and Ord kangaroo rats have been observed to increase the efficiency of contour furrows, but to endanger contour dykes by providing

channels through which water may flow (Compton & Hedges 1943).

Soil Moisture Relations

Soil moisture is usually the factor limiting plant growth on the lands inhabited by Merriam kangaroo rats. Modification of soil properties to increase absorption and retention of rainfall is reflected in superior plant growth. Some indication of the effect of these animals upon soil moisture relations was obtained by measuring the effect of burrowing upon the water-holding capacity and moisture infiltration relations.

Effects on the Moisture Holding Capacity. This soil property was measured indirectly by determination of the moisture equivalent. Soil samples were taken to a depth of 12 in, under mesquites having a burrow, and under adjacent mesquites where there was no burrow.

The presence of a burrow had no consistent measurable effect upon the moisture equivalent of the soil (Table 6). Evidently, soil disturbance resulting from the construction of a burrow is insufficient to change this soil property. The greater burrowing activity of bannertail kangaroo rats has been observed, however, to have a significant effect upon the physical properties of the soil as expressed by the moisture equivalent. Burrowing activities of these animals tend to comminute the soil, and give rise to a larger percentage of finer soil particles (Greene & Murphy 1932).

TABLE 6. Effect of burrowing by Merriam rats upon moisture equivalent and infiltration relations of the soil.

Burrow Number	Center of Burrow	Adjacent Bare Area	Remarks
	Moisture Equivalent (%)		
1	8.4	8.4	Beneath mesquite
2	9.5	10.6	Beneath mesquite
3	9.9	9.9	No protective shrubs
4	11.5	11.2	Under burroweed
5	10.9	10.9	Under burroweed
6	10.0	10.0	Under cactus
	Infiltration in cc/sec		
1	3.0	2.8	Under mesquite
2	2.0	0.5	No shrubs
3	2.5	1.6	Burroweed only
4	3.8	1.0	Burroweed only
5	2.7	0.6	Cactus and burroweed

Effects on Infiltration. This soil characteristic was measured by the method of Auten (1933). In the center of the burrow, within a zone of influence of 2 ft, the rate of infiltration was higher than on adjacent undisturbed soil (Table 6). Except where the burrows were located under a mesquite, the rate of infiltration in the center of a burrow was two to four times as rapid as it was on adjacent undisturbed areas.

The maximum increase in infiltration rate was 2.8 cc/sec in a zone of influence of 3.14 sq ft/burrow. With about 20 burrows/acre, a total of about .015% of an acre would be affected. Moreover, most burrows are located beneath mesquites, and the effect of the latter upon promoting infiltration is as great as burrowing. Hence, the total effect of the burrowing activity of Merriam kangaroo rats upon raising the infiltration capacity of the soil is negligible.

RELATION TO LAND USE (LIVESTOCK GRAZING)

Most of the lands inhabited by Merriam kangaroo rats are managed primarily as rangelands for cattle grazing. Water yield is low from these areas, but sediment yield is high. Whether to furnish grazing or to reduce erosion, these lands must be managed so as to maintain the best plant cover. On the higher lands, maintenance of a perennial grass cover with an interspersion of shrubs best meets both objectives. At the lower, drier elevations a shrubby cover is all that can be maintained practically.

A perennial grass or desirable shrubby cover is achieved through proper grazing practices with cattle and attention to suitable range improvement practices. The relation of Merriam kangaroo rats to these practices determines largely the attitude which must be adopted towards these animals.

Relation to Grazed Rangelands

When rangelands are properly grazed, perennial grass density changes in response to rainfall variations but fluctuates about an average density for the normal growing conditions for the site. When rangelands are improperly grazed, there is a gradual downward trend in perennial grass density.

Merriam kangaroo rats are more abundant on ranges grazed by cattle. Grazing not only reduces the stubble height of grasses, but when it is continuously heavy over several years it also reduces the density of perennial grasses. Both of these influences make the habitat more favorable for Merriam kangaroo rats and their numbers increase as a result.

A series of range revegetation plots offered an opportunity to determine whether or not the seed planting activities of Merriam kangaroo rats were sufficient to be detected by plant measurements. The original data which furnished the basis for these conclusions can be found in Reynolds (1950). The plots were established by the University of Arizona and were measured carefully each year. One series of exclosures was protected against rodents; the other was open to rodent activity. Merriam kangaroo rats were the prodominant rodents on the area, were among the few animals known to live almost entirely upon seeds, and were the only rodents which use surface caches for seed storage. Accordingly, any rodent influence with regard to plant reproduction can be attributed mostly to Merriam kangaroo rats.

The results of analyzing the plant establishment on these revegetation plots were as follows: (1) Seedling establishment of annual plants and small-seeded perennial grasses showed little relation to

Merriam kangaroo rat abundance. (2) Large-seeded perennial grasses and tall shrubby plants (mesquite and cholla) increased markedly on plots where these rodents were most abundant. Presumably, kangaroo rats stored considerable seed in excess of needs. Being in a more favorable soil environment for germination and survival, seed germination and seedling establishment were superior. Thus, in a good seed year, when seed is stored in amounts in excess of needs, these rodents favorably affect dispersal and germination of seeds of large-seeded perennial grasses and tall shrubby plants. Hormay (1943) noted a similar planting relation between the chipmunk and golden mantled ground squirrel, and bitterbrush in northeastern California. Spread and increase of bitterbrush was greatly favored by the work of these rodents in planting seed in surface caches.

Relation to Range Condition

Range condition refers to the productivity of grazing lands relative to the highest production attainable for a particular site. Deterioration of desert grasslands from top production is caused by two main factors—improper grazing, and the invasion of woody plants. When grazing is improper over a long period, a change in grass composition occurs. This change is followed by a loss in perennial grass density. Continued misuse can lead to the complete disappearance of perennial grasses, and their replacement by annual plants.

Three groups of invading woody plants are contributing to the deterioration of grazing lands on the Santa Rita Experimental Range. The most important is velvet mesquite *(Prosopis juliflora)* (Glendening 1949). This plant seems to be increasing in abundance whether ranges are grazed by domestic livestock or not. Since 1932, cactus *(Opuntia* spp.) has in some localities increased as much as 500 plants/acre and livestock grazing seems to be an important factor in its spread and increase (Glendening 1952). Burroweed *(Aplopappus tenuisectus)* has also increased sharply, but as with mesquite there seems to be no strong connection between burroweed increase and the grazing of domestic livestock (Brown 1950).

Increase of woody plants, particularly velvet mesquite, is accompanied by a decline in perennial grass density. Mesquite uses soil moisture which would otherwise be available for perennial grasses. This relation has been demonstrated on experimental plots cleared of mesquite. Where there was sufficient perennial grass cover to respond, four-and five-fold increases in perennial grass were observed a few years after elimination of mesquite (Parker & Martin 1952). As perennial grass cover decreases, range condition or productivity of the site for cattle grazing is lowered.

Merriam kangaroo rats bear a reciprocal relation to perennial grass density (Reynolds 1950). As grass increases rats decrease. Heavy perennial grass vegetation provides an unfavorable habitat for these rodents by interfering with their mode of escape. A scant cover of perennial grass favors rapid and hasty retreat to a shrub or escape burrow.

Other species of kangaroo rats also avoid dense herbaceous vegetation. Hawbecker (1940) noted that the dens of *Dipodomys venustus* were characteristically found in the open and that the species seemed to avoid areas occupied by chaparral. The Tulare kangaroo rat exhibits awkwardness in thick vegetation and prefers open situations (Fitch 1948). Dale (1939) also observed that *D. h. saxatilis* because of its instincts and morphological characters was placed at a disadvantage in dense cover.

There is no relation between numbers of mesquite and Merriam kangaroo rats. Mesquite-infested areas can be found where no rats are present, and Merriam rats are often abundant where there is no mesquite. Although mesquites furnish a favored location for burrows, the most important relation of these trees to kangaroo rats is indirect, through making the habitat more favorable by reducing the density of perennial grass (Reynolds 1954).

The interrelations of mesquite, perennial grass, and kangaroo rats make possible some deductions as to how these animals are related to range condition. When a range is in good to excellent condition, Merriam kangaroo rats have little effect upon range condition. At this stage, changes in plant composition may occur, but a downward trend in grass density which would affect kangaroo rat numbers is unlikely. Mesquite seed may be planted by rats, but this method of dispersal is slow and measures can be adopted for suppressing the increase (Parker & Martin 1952).

As a range deteriorates to fair or poor condition, Merriam kangaroo rats increase, and their presence becomes more important, especially if an increase in mesquite is associated with the decline in range condition (Fig. 9A). When perennial grass declines the habitat becomes increasingly favorable for kangaroo rats and mesquite. When the cycle of more mesquite—less perennial grass—more rats—more mesquite is well advanced, Merriam kangaroo rats become an important factor in accelerating range deterioration.

In advanced stages of deterioration (poor to very poor condition), Merriam kangaroo rat activity may be sufficient to prevent range recovery even though cattle grazing is completely removed (Fig. 9B). Many perennial grasses produce preferred seeds. When the seed supply is sufficiently low, Merriam kangaroo rats may consume the entire seed supply. Moreover, if mesquite trees are fairly abundant, these plants will continue to increase, aided by kangaroo rats, even when cattle grazing is eliminated (Reynolds & Glendening 1949).

If range condition is at a level where the seed supply of large-seeded perennial grasses is in excess of the needs of Merriam kangaroo rats, these animals can be a beneficial influence provided mesquite is not abundant. Much seed, in excess of needs, is gathered and stored in the surface soil. This seed is in a more

FIG. 9. Interrelations of mesquite, perennial grass and numbers of Merriam kangaroo rats. (*A.*) A rangeland commencing to deteriorate as a result of improper grazing and mesquite invasion. Kangaroo rat numbers are moderate, and restoration could be achieved by removing mesquite and adjusting livestock numbers. (*B.*) Rangeland deterioration is complete. Perennial grasses are destroyed and mesquite has completely occupied the site. Kangaroo rat population is high.

favorable environment for germination than that deposited on top of the ground by wind and gravity. Ranges recovering from drought actually improve faster initially as a result of Merriam rat activity. However, where mesquites are abundant, the beneficial effect of planting perennial grass seed may be overshadowed by the undesirable spread of mesquite seed (Fig. 10).

RELATION TO RANGE IMPROVEMENT

Maintenance of desert grasslands in a highly productive state requires continual attention to measures for preventing site deterioration or for restoring site productivity. This often means providing for reseeding and woody plant control.

Range Reseeding. Rangelands severely depleted of perennial grass, yet still basically productive, so that self-restoration in a reasonable length of time is impractical, can be benefited by range reseeding. Since this practice requires considerable investment in the land, the relation of Merriam kangaroo rats to range reseeding is an important consideration.

Merriam kangaroo rats discover and consume buried seed. Size of seed seems to be the major factor limiting discovery. Reseeding plantings are usually made during May and June when the supply of native seed is scarce. Seed is seldom planted

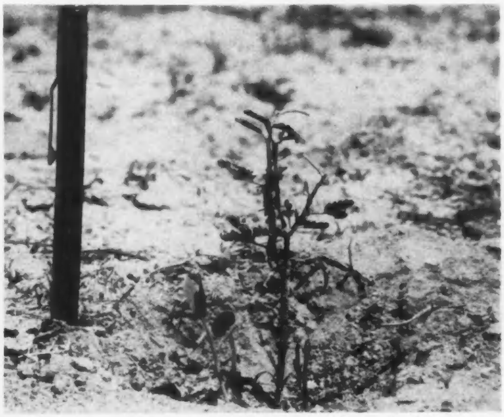

FIG. 10. Mesquite distribution and survival is benefited by Merriam kangaroo rats. Not all mesquite seeds in a surface cache sprout simultaneously. Seedlings in this cache are from 1 to 3 years of age.

deeper than 1 in, and these rats easily locate large-sized seed at this depth. Around small plantings, destruction of seed is often severe.

If seed smaller than 500,000 seeds/lb is planted the effect of Merriam rats is insignificant. If larger seed is planted, reduction of rat numbers is not only justified, but a wise investment. Small row plantings of large-seeded shrubs on the Santa Rita Experimental Range have been almost completely excavated within a week by these animals. The expense of reducing rat populations in relation to the other costs of reseeding is small. Where large-seeded species are used, control of Merriam rats may mean the difference between success and failure of a planting.

Woody Plant Control. Of the three forms of woody plants, burroweed, cactus, and mesquite, only the latter seems to bear an important relation to numbers of Merriam kangaroo rats. These animals are an unimportant factor contributing to the spread or increase of burroweed, because seeds of this plant seem to be avoided. Cactus seeds are disseminated by kangaroo rats. High populations of rats are not, however, necessarily associated with greatest numbers of cacti. Moreover, the presence of cacti does not improve the habitat for kangaroo rats. In general, factors more important than kangaroo rats are responsible for the increase and spread of cacti.

If rangelands occupied by mesquite are grazed by cattle, mesquite will increase (unless control measures are employed) whether Merriam kangaroo rats are present or not. Cattle serve as an effective and important distribution agency for mesquite. Removal of Merriam rats may slow the rate of increase of mesquite, but cattle and other dispersal agencies will continue to disseminate the seed; and the range will eventually be fully occupied with mesquite (Reynolds 1954).

Merriam kangaroo rats are not the only factor or agency responsible for the increase of mesquite. The relation between rats and mesquite is not a de-

pendency one. Rats inhabit land where mesquite will not grow and mesquite occupies sites where these animals do not occur. The relation is one of commensalism. Rats take advantage of the improved habitat afforded by the presence of mesquite, and the distribution and dissemination of mesquite is benefited by but not dependent upon the presence of the rats. Removal of mesquite from rangelands destroys the cause of the infestation, and does not attempt to treat it. On practical grounds removal of mesquites, thereby destroying the source of seed, is much wiser than any attempt to manipulate the dispersal agencies. Once mesquite is removed the effect of dispersal agencies is automatically eliminated. In addition, when mesquite is destroyed, perennial grasses increase in abundance, which automatically reduces Merriam kangaroo rat numbers, because of the less favorable habitat produced.

SUMMARY

This study reports some life history, habitat, and economic relations of the Merriam kangaroo rat *(Dipodomys merriami)* for the Santa Rita Experimental Range and similar rangelands of southern Arizona.

The area is characterized by limited rainfall. Greatest rainfall and highest temperatures occur during the summer, lowest rainfall and intermediate temperatures during the fall and spring, and low temperatures and intermediate rainfall during the winter. This type of climate results in poorly developed soils and a vegetation composed of desert shrubs, drought resistant, summer growing perennial grasses, and annual plants, some of which mature in the spring, others in the summer.

The main factors limiting geographical and elevational distribution of the Merriam kangaroo rat appear to be heavy textured or rocky soil, a blanket of snow, high rainfall, low temperatures, and a high density of perennial grass.

Annually, numbers of rats were highest in July when immature animals were most abundant. Yearly variations from 7.0 animals/acre in the winter of 1950 to 1.4 animals/acre in the winter of 1946 were observed. Direct and indirect effects of precipitation seemed to be the most potent factors determining animal numbers.

About 95% of the items occurring in cheek pouches are seeds. Kind of seed collected varies in order of abundance seasonally and annually somewhat in accordance with availability. To maintain body weights, where activity is reduced to a minimum consistent with good health, Merriam kangaroo rats were found to require about 5 g of rolled barley/day.

During vegetational seeding periods, Merriam kangaroo rats store much seed in surface caches which are covered to a depth of 1-2 in. Many caches are relocated during fall, winter, and spring. Seed in those caches not rediscovered may sprout during favorable rainy seasons.

These rats do not have a large influence upon soil cultivation, because the burrowing adaptation is poorly developed. Burrowing has no effect upon moisture equivalent, and a negligible effect upon infiltration.

Within their altitudinal range, Merriam kangaroo rats are more abundant on ranges grazed by domestic livestock. Grazing so heavy as to lower perennial grass density results in an increase in their numbers. On rangelands in good to excellent condition, the seed burying habits of Merriam kangaroo rats are probably beneficial to range maintenance and improvement. On the other hand, the spread of mesquite and cactus on infested range is favored somewhat by the presence of these animals.

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THE FLOOD PLAIN OF THE RARITAN RIVER, NEW JERSEY

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INTRODUCTION

The flood plain of the Raritan River in New Jersey is usually less than 0.5 mi. in width and occurs throughout much of the length of the river. It has been extensively used for cultivation or for pasture, leaving little or no woodland entirely free from disturbance. At a few places along the river there are areas which give some indication as to the natural composition of flood plain and adjacent terrace forests. Some of these forests have been described by Buell & Wistendahl, 1955. At other places successional trends on islands, river banks, and abandoned fields are evident. This study includes several aspects of the flood plain and its vegetation, ranging from early successional stages to the most mature forests as found here.

The Raritan River drains about 1,105 sq. mi. of central New Jersey (Vermeule 1894). Its numerous branches and tributaries extend into three of the four geologic provinces of the state: namely, the Coastal Plain, The Piedmont, and the Highlands (Fig. 1). Two major branches of the river originate in the Highland Province on or near the Wisconsin terminal moraine. The North Branch, which joins with the Lamington River near Burnt Mills (elev. 60 ft), flows southward from the Highlands onto the Piedmont. The South Branch, originating in Budd Lake (elev. 933 ft) about 5 mi. west of the source of the North Branch, flows southwesterly and then loops easterly joining the North Branch near Raritan, New Jersey (elev. 50 ft), where they then form the main easterly flowing river. Near Manville the north flowing Millstone River joins the main body of the Raritan which continues easterly, passing New Brunswick and emptying into the Raritan Bay.

At the confluence of the Lamington River with the North Branch at Burnt Mills a flood plain has developed which has some relatively undisturbed wooded areas. Where the North Branch joins the South Branch, a similar but more extensive flood plain has developed at Raritan, New Jersey. The forests on these two flood plain areas contain the oldest trees. Along the north side of the lower part of the Raritan River near New Brunswick there is a rather extensive flood plain. The south side of the river has been used for the construction of the Delaware-Raritan Canal and flood plain areas there have thus

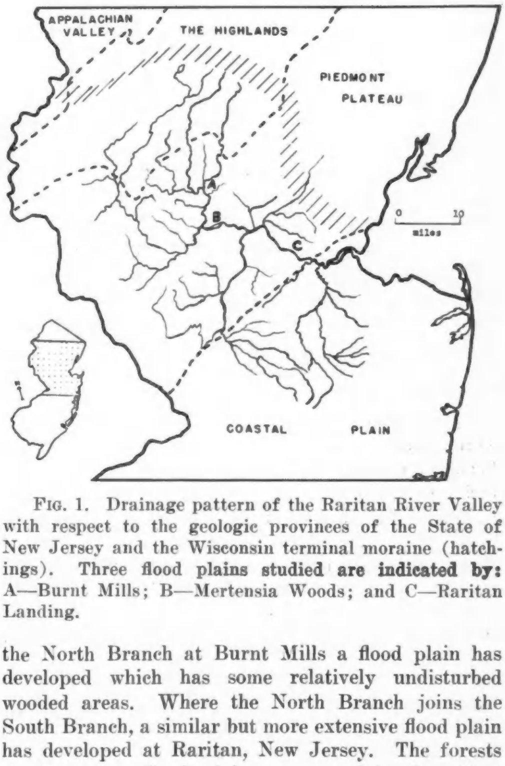

FIG. 1. Drainage pattern of the Raritan River Valley with respect to the geologic provinces of the State of New Jersey and the Wisconsin terminal moraine (hatchings). Three flood plains studied are indicated by: A—Burnt Mills; B—Mertensia Woods; and C—Raritan Landing.

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been cut off from the river. The flood plain on the north side at this vicinity has been used in the past as mill, warehouse, docking, and agricultural sites (Vermeule 1936). At present recreational parks occupy some of the area, while other portions are in various stages of revegetation.

The two principal branches of the Raritan River flow over geological formations which are similar (Lewis & Kümmel 1912). They both arise on or near the terminal moraine of the Wisconsin glacier. At their sources glacial drift covers much of the underlying Pre-Cambrian gneisses. Flowing down from these resistant ridges, the branches cut across or follow occasional beds of Cambrian sandstone and Cambro-Ordovician limestone. Drainage from small areas of Ordovician shale and Silurian conglomerate flows into the North and South Branches. Before flowing onto the extensive Triassic red shale and sandstone valley, the South Branch and the Lamington River cross a small section of Triassic conglomerate. Once on the Triassic shales and sandstones the river remains on such material to its mouth, except for some drainage from old glacial drifts (Jerseyan?) which form high river-terrace deposits. The river ultimately flows into an estuary which has developed on Cretaceous materials.

The Millstone River originates partly on Cretaceous and partly on Triassic deposits. It cuts across a ridge of diabase of Triassic age and, flowing northward, joins the Raritan River near Manville. Other tributaries of the Raritan River drain some areas of both diabasic and basaltic igneous rocks of the same age (Triassic). These rocks are, for the most part, the Cushetunk and Watchung Mountains. Because the river cuts across a variety of bed rock types, some dating back to Pre-Cambrian time and some as recent as the Cretaceous. There is a great variety of source materials for the alluvium of this relatively short system.

Investigation of the flood plain was made during the years 1952, 1953, and 1954. Three general areas were studied in detail (Fig. 1). These were on the flood plain below the junction of the North Branch and the Lamington rivers, which will be referred to as Burnt Mills area (lat. 40° 37.2′ long. 74° 40.5′); on the flood plain below the junction of the North and South Branches of the Raritan near the town of Raritan which will be referred to as Mertensia Woods (lat. 40° 31.1′ long. 74° 39.5′); and on the flood plain near New Brunswick, which is part of an area known as Raritan Landing (lat. 40° 31.3′ long. 74° 28.5′). A flood plain, although a single physiographic feature, possesses a varied topography with equally varied local vegetational patterns. These patterns intergrade from place to place but nevertheless are distinctive enough to be recognized as composed of plant communities. Several such plant communities were sampled independently to bring out vegetational differences which would be lost in less discriminate sampling.

I wish to express my appreciation to Dr. Murray F. Buell for his guidance of this study and to Mr. Malcolm J. Smith of South River, New Jersey, for his assistance in the field obtaining transit data. For the use of unpublished data, I am grateful to Messrs. A. E. White, O. W. Hartwell, E. G. Miller, and O. Lauterhahn of Trenton, New Jersey.

DISCUSSION OF THE LITERATURE

Flood plain forests possess luxuriant vegetation (Cowles 1901, Nichols 1916, Humphrey 1924, Gordon 1936, Lee 1945). Changes in composition are frequent although the same general list of species prevails throughout a river flood plain system. Lee (1945) found that even though the flood plain of the White River system in Indiana dissected different geologic provinces, each with its own characteristic vegetation, the same flood plain species persisted. He concluded that dominance of one or a few species was not evident. Turner (1936) found that the flood plain forest of the lower Illinois River had more tree species with a dominance index (frequency multiplied by density) over 100 than any other forest he studied in the lower Illinois valley, although silver maple *(Acer saccharinum)* and American elm *(Ulmus americana)* were the chief dominants. Core (1929) considered the herbs of West Virginia flood plains to be "mainly Carolinian (Upper Austral), with a good sprinkling of Alleghenian (Transitional) species." Oosting (1942) summarizes that "slight variations in topography and drainage have pronounced effects upon moisture conditions in bottomlands" and that bottomland communities are ". . . often made up of mixtures of species . . ."

Cribbs (1917) called the flood plain forest of western Pennsylvania a mesophytic forest. Cowles (1901) saw no reason why mesophytic forests should not develop on the flood plains in the Chicago area, with a trend toward retrogression with terrace formation. He was impressed by the number of kinds of trees such as tulip tree *(Liriodendron tulipifera)* which were not common in the Chicago district. Braun (1916) refers to the "high level flood plain" of the Cincinnati region as bearing a mixed mesophytic forest. The continual formation of new surfaces led Shelford (1954) to believe that flood plains are "exceptionally useful, and perhaps as important as sand areas in the study of ecological principles."

The various and variable habitats of river flood plains, bottomlands, and terraces where differences of topography, drainage, light and other factors are interacting present interesting ecological problems. Oosting (1942) recognized that moisture relations on bottomlands influence stand development. Controlled experiments by McDermott (1954) on the "effects of saturated soil on seedling growth" show that the bottomland species which were observed by Oosting recover from the effects of soil saturation at varying rates. Illickevsky (1933) refers to the importance of rivers in controlling distribution of plants. He lists species which are restricted to regularly flooded zones or to higher grounds along various rivers in Russia. The successional trends found on the upper Missis-

sippi River by Barclay (1924) were observed by Hefley (1937) on the Canadian River. Russell (1953) in studies of the Apple River Canyon of Wisconsin states that "almost every step along the bank of the river took one into a different society." Hefley (1937), Goff (1952) and Shelford (1954) worked out interesting studies of flood plain animal communities, based largely upon the developmental aspects of flood plains within the areas studied.

Many of the aspects of flood plains have been studied by various workers, investigating the effects of silting on tree development (Harper 1938) and on forest succession (Featherly 1941); island formation and development (Shull 1922, 1944); permanent flooding (Yeager 1949); vegetation (Stallard 1929, Hotchkiss & Stewart 1947, Penfound & Hall 1939, Burns 1941, Ware & Penfound 1949, Turner 1930, 1934, Conard 1952, and Griggs 1914) and geographical aspects (McGee 1891).

METHODS

Quantitative data for the herb layer at Burnt Mills were obtained from forty 0.5 x 2 m quadrats in each of 3 plant communities, the outer flood plain, the inner flood plain and the terrace. These quadrats were located at 10 m intervals along 4 transect lines at each unit. The herbaceous cover in Mertensia Woods was studied in the same manner. The percent cover for herbs, mosses and litter was estimated for each quadrat. Lack of cover was recorded as space. Seedlings (less than 1 ft tall) of tree species were counted on all quadrats. Data were obtained during late May and early June and again in late August and early September.

Several transects cutting across the flood plain perpendicular to the river at Burnt Mills, Mertensia Woods and Raritan Landing were studied. Data for descriptive purposes and for comparing vegetation on various parts of the flood plain were obtained along these lines. Cover was estimated for each 10 m segment of the line and at 10 m intervals a careful search was made for tree seedlings as well as noting the size and abundance of saplings and trees.

The methods described below apply to the study of 3 revegetated fields at Raritan Landing. These fields were covered by different densities of woody species and had obviously ceased to be used agriculturally at different dates. The line intersect method was used (Buell & Cantlon 1950). A 400 m line was used on the youngest or most recently revegetated field but a 200 m line was used on the other fields because of their smaller size. The transects traversed the length of the fields and consequently ran parallel to the direction of the river. Two or three parallel lines were used, depending on the size of the field.

Tree cover and sapling and shrub cover were determined along the entire length of each transect. (The term sapling is used for individuals of tree species which are less than 1 in. d.b.h. and over 1 ft. tall.) At 5 m intervals along each transect line the percent cover was estimated for herbs and tree seedlings were counted on ½ x 2 m quadrats. The diameters of all trees greater than 1 in. d.b.h. were measured within 1 m of each side of the transect lines. Data were recorded for successive 10 m segments of transect. Similarly the number of saplings within ½ m of the lines were counted for each 10 m segment of line. This, in effect, resulted in a series of nested quadrats which were 2 x 10 m in size for trees and 1 x 10 m for saplings, with two ½ x 2 m herb quadrats per nest.

The river bank vegetation bordering the fields at Raritan Landing was sampled at two areas by a combined quadrat-cover transect method. One series of 15 quadrats and cover transect was obtained adjacent to the youngest and intermediate revegetated fields. The second series was of 5 quadrats adjacent to the oldest field, which was farther upstream.

The 10 x 10 m quadrats were placed so that they lay entirely on the bank sloping down to the river or to the reed canary grass *(Phalaris arundinacea)* fringe along the river. In each 10 x 10 m quadrat on the upper part of the bank one 2 x 10 m and two ½ x 2 m quadrats were included. Tree diameters (d.b.h.) were recorded for each 10 x 10 m quadrat. Tree saplings were counted in the 2 x 10 m quadrat, and tree seedlings were counted in the ½ x 2 m quadrats. The percent herbaceous cover was estimated in each of the smallest quadrats.

Cover of trees, saplings, and shrubs were obtained by the line intersect method. A 20 m tape was extended diagonally across each 10 x 10 m quadrat. Thus each line crossed the bank at an angle of about 45° to the river.

The transect method was also used for sampling the reed canary grass area which borders the river between the water and the bank of the natural levee at Raritan Landing. About midway between the bank and the water a 200 m line was established. Details for sampling were the same as those described above for transects cutting across the flood plain.

Heights of trees were determined with the use of an Abney level. Ring counts were determined from borings or from freshly cut saplings and recently cut trees.

Cover values obtained by use of transects can be expressed as the percent of the length of transect covered by the total crown spread of individuals of one species, or by the percent each species contributes to the total cover (length of transect minus unoccupied space) of all species along the transect. Because of the overlap of crowns, the former method of expression may, when the percentages of all species are added, total greater than 100%. However, the latter method of expression will total 100%. Thus, cover computed on the basis of the length of transect covered by the total crown spread of individuals of one species will be referred to as actual cover, and cover computed on the basis of total cover of all species will be referred to as relative cover. Relative cover values will be used in this paper unless stated otherwise.

Soil on flood plains is extremely variable in texture from one area to another. To bring out the difference in soil composition with increased distance from the river, 3 series of 4 samples each from the upper 10 cm were obtained at points across the Raritan Landing area near New Brunswick for mechanical analysis (Bouyoucos 1936). Thus 4 came from the natural levee close to the river, 4 from the marshy area behind the levee, and the others from about half way between.

Near the middle of the levee at Raritan Landing a soil pit was dug to the water table, which at the time was at a depth of about 6 ft. The thickness of deposits of gravel, sand, silt, and clay were measured. Notes were made on soil color, pebble content, and root penetration.

Three cross section profiles of the flood plain were obtained by use of an engineer's transit. These profiles were taken at the Burnt Mills area, Mertensia Woods and Raritan Landing.

GENERAL FEATURES OF FLOOD PLAINS

The dynamics by which fertile flood plains are developed have been frequently described (von Engeln 1948, Longwell *et al.* 1948, Cribbs 1917, Nichols 1916, Sallards *et al.* 1923). Basically two main processes are concerned: degradation—the eroding of river beds and banks—and aggradation—the desposition of eroded materials at some point farther downstream. During floods, especially during the falling stages, as the velocity of the river decreases, the heavier particles of sand are deposited near the river's edge, and the lighter particles of clay and silt are deposited a greater distance from the river's edge. This sorting out of materials results in differential rate of flood plain development so that a natural levee builds up near the river's edge and a lower area develops behind it.

The valley slope, bed-load, discharge, bed resistance and the transverse oscillation of the water at the surface of a river greatly influence the meander pattern of a river. The inability of a river to adjust its width in accordance to its velocity leads to alternate deposits of sand bars, first on one side of the river and then on the other. These deposits cause the river water to be diverted first toward one bank and then toward the other, developing a serpentine course or meander pattern (Matthes 1941). The meander of a river across resistant bed rock or across previously deposited flood plain materials gives a usually slow changing but nevertheless dynamic aspect to flood plain communities.

Samples of river bank, field, and marsh soils taken at Raritan Landing show remarkable differences in composition upon mechanical analysis (Fig. 2). These differences reflect the dynamics of deposition during floods.

Certain soils of the flood plains of the Raritan River are mapped as a Bermudian silt loam (Patrick *et al.* 1923), a fertile, well-drained soil. A more recent survey shows the flood plain soil to be a catena

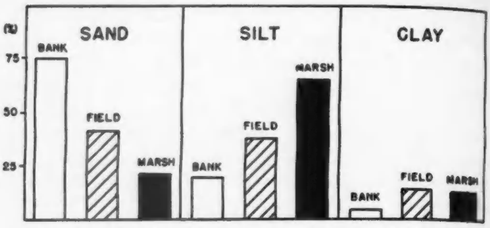

FIG. 2. Results of the mechanical analysis of soil sampled at 3 distances from the river at Raritan Landing: river bank 10 m, field 80 m, marsh 170 m. Each value is the average of 4 samples from the upper 10 cm at each location.

ranging through the well-drained Bermudian, imperfectly drained Rowland[2] and poorly drained Bowmansville[2] soil series. Although only at Raritan Landing was the soil studied intensely for this present study, observations at other places along the river showed similar variations. The large variety of geologic material from which this soil was derived and the differences in degree of flooding at various places along the river result in soils heterogeneous in composition.

The flood plain areas along the Raritan River have been mapped from aerial photographs (Fig. 3). The meander pattern of the river is irregular due to resistant red shale outcrops and glacial drift deposits which are encountered at various places along the river. This irregularity tends to make each flood plain area different in size from the next, as the height of the river banks and thus the intensity of flooding vary greatly.

The soil pit dug in a field at Raritan Landing shows in its vertical profile the development of the flood plain of the Raritan River at that point (Fig. 4). The ancient river bed encountered at the bottom of the pit was of rocks similar in size and shape to those of the present day river bed (Fig. 5). This would suggest that, at the point where the pit was dug (about 80 m from the edge of the river) the river used to flow at about the same rate as it does today. As the course of the river moved farther from this point, stream velocity decreased and first gravel, then sand, became deposited over the large river bed materials. When the deposit was built to a depth of about 2 ft, a thin layer of silt and clay was laid down. This indicates the possibility of a continued migration of the stream away from the site of the pit. The deposition of gravel and sand above this layer could mean that the stream meandered slightly back toward the site of the pit, or that the velocity of the stream increased, carrying coarser particles farther back on the then existing flood plain. Deposits lying on top of this sand and gravel show a decrease in sand and an increase in silt and clay to the surface of the present day flood plain. Occasional larger-sized pebbles in the

[2] Local names not officially correlated by the soil survey division of the U.S.D.A.

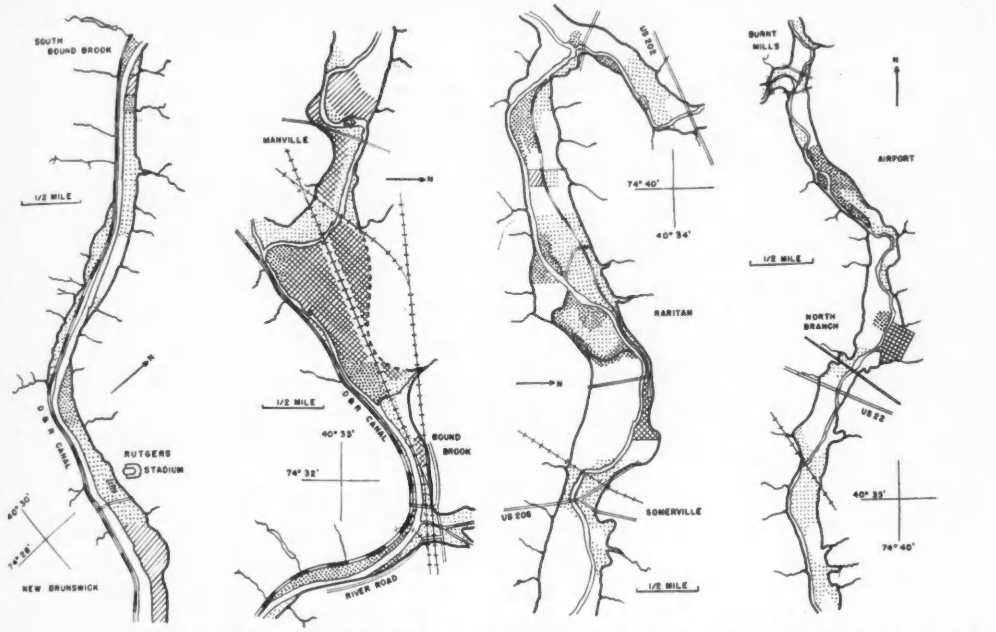

FIG. 3. The flood plain of the Raritan River between New Brunswick and Burnt Mills showing location of agricultural land (blank spaces), heavily wooded areas (heavy dots), sparsely wooded areas (light dots), industrial sites (cross hatching), and recreational areas (diagonal hatching). Mapping is continuous, progressing upstream from the lower left hand corner to the upper right.

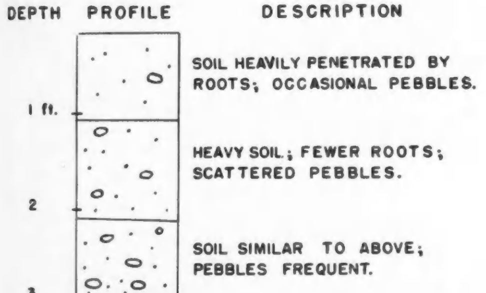

FIG. 4. Diagrammatic interpretation of soil profile 80 m from the river at Raritan Landing.

upper part of the profile may be the result of sporadic heavy floods.

At Raritan Landing the developmental history of the existing flood plain seems to be one of almost constant deposition as the river meandered in a southerly direction away from the resistant red shale outcrop upon which the Rutgers Stadium has been built. One period of meander reversal or of increased river velocity seems evident.

Vermeule (1894) indicated that a river discharge of 7,000 cu ft per sec (sec-ft) was considered a full bank stage at Bound Brook. By interpolation this is equal to a discharge of about 4,000 sec-ft at the Manville station which is 4.5 mi below the confluence of the North and South Branches. This station has the longest and most complete records of daily discharges. On the basis of Vermeule's statement, discharges over 4,000 sec-ft or their equivalent in gage height are considered floods.

Although the patterns of flooding, precipitation, and temperature show great irregularity from one year to the next, certain trends are evident (Fig. 6a). There were usually more days of flooding and longer periods of flooding prior to 1921. During that period many of the early yearly averages of temperature fall below 52°F which is the 1930 average. The total yearly precipitation was generally greater prior to 1921 than later. On the other hand the trend since 1921, even though slight, is toward higher temperature, lower rainfall, and fewer floods. Nevertheless, the yearly number of floods on the Raritan River is extremely variable and unpredictable, sometimes totalling 16, more frequently much less, and sometimes none.

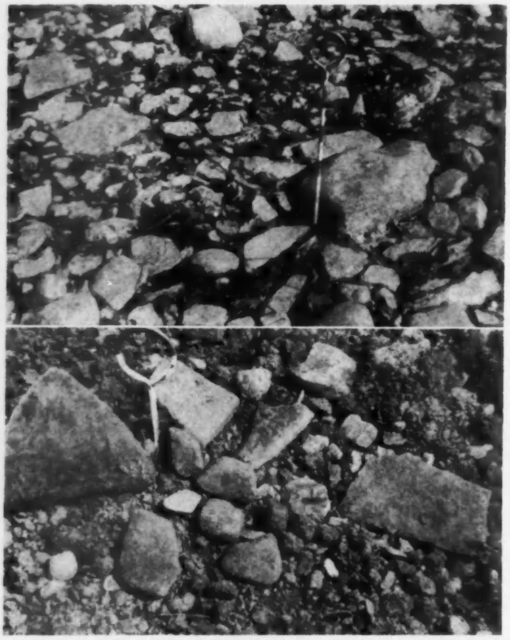

FIG. 5. The upper photograph shows the river bed of the present course of the Raritan River near Raritan Landing. The lower photograph shows material of an ancient river bed removed from the bottom of the soil pit on the natural levee at Raritan Landing.

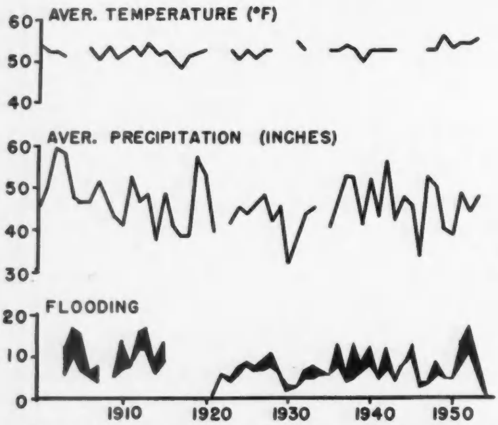

FIG. 6a. Temperature, precipitation, and flooding by year in the Raritan River Valley. The width of the darkened band in the curve for flooding indicates the intensity of flooding. The upper limit of the band represents the number of days of flooding; the lower limit, the number of floods for each year of record. When the band narrows to its thinnest width, floods were only one day in duration. Data from published and unpublished records at Trenton, N. J.

The seasonal distribution of floods (Fig.6b) on the Raritan River shows that the season with the greatest number of floods is not during the months with the highest average monthly precipitation (July and August, 4.8 in.). Rather, the number of days of flooding is at a maximum in March and the floods are often a few days in duration. This is undoubtedly the result of spring rains, sometimes on frozen soil and in some years with melting snow.

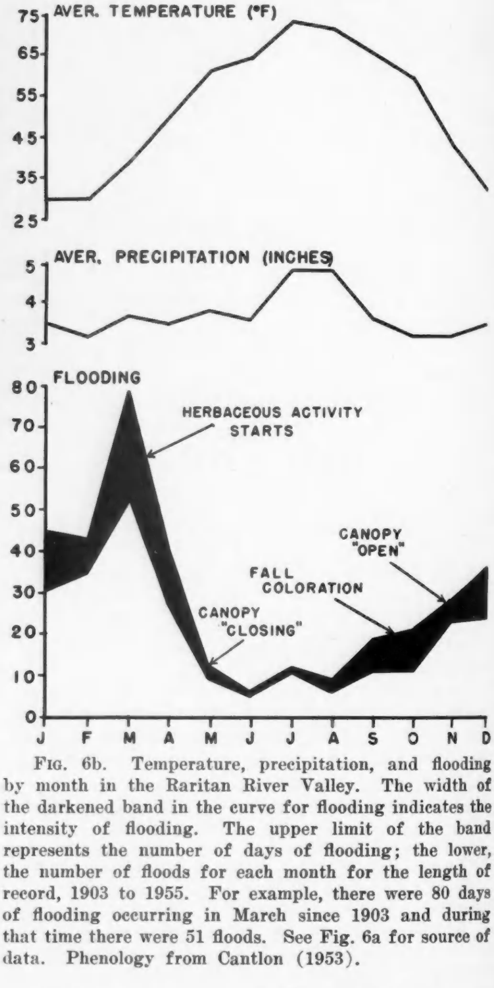

FIG. 6b. Temperature, precipitation, and flooding by month in the Raritan River Valley. The width of the darkened band in the curve for flooding indicates the intensity of flooding. The upper limit of the band represents the number of days of flooding; the lower, the number of floods for each month for the length of record, 1903 to 1955. For example, there were 80 days of flooding occurring in March since 1903 and during that time there were 51 floods. See Fig. 6a for source of data. Phenology from Cantlon (1953).

As the season progresses from spring to summer, there is a sharp drop in the number of floods to a yearly low in June and August. During this time less water is available for runoff, as much soil water is utilized by actively growing plants. In addition, there is an increase in the interception of rainfall by foliage as the tree canopy closes, which might average as much as 20%-30% in forested sections of a watershed (Kittredge 1948). Also higher temperatures increase the rate of water loss by evaporation. A reduction in the number of floods occurs, despite the fact that the average monthly precipitation is greater during the summer.

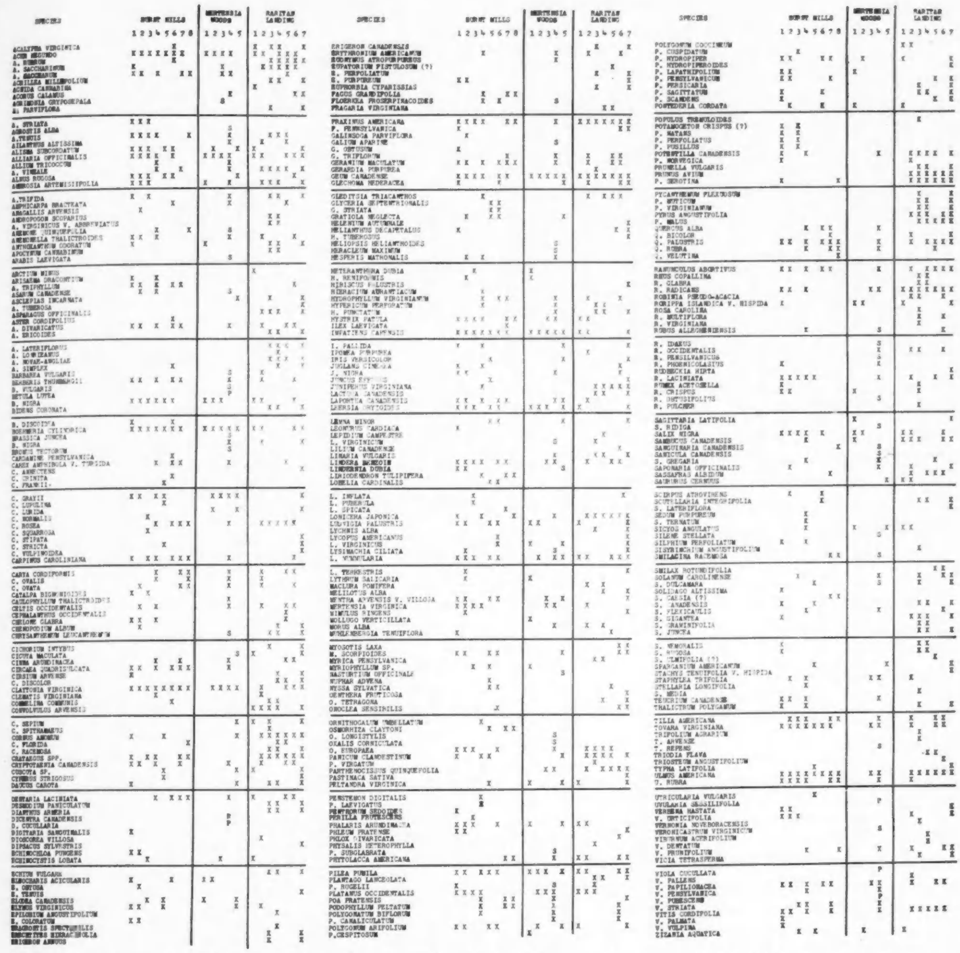

FIG. 7. General distribution of species according to habitat on 3 areas of detailed study, omission of species from any one habitat does not preclude its presence. Habitats and occurrence based on quadrat, transect, and reconnaissance data. Species marked S are from a species list contributed by Dr. J. A. Small of Douglass College; those marked P, by Dr. Grace A. Petersen of Brooklyn Institue of Arts and Science. Habitats for the Burnt Mills area are: 1—Island A, 2—Island B, 3—River banks, and river margins, 4—Outer flood plain, 5—Deep sloughs, 6—Shallow sloughs, 7—Inter-sloughs and 8—Terrace. Habitats for Mertensia Woods (Mertensia "island") are: 1—River bank, and river margins, 2—Sloughs near the river, 3—Inter-sloughs, 4—The Woods and 5—Deep slough behind the Woods. Habitats for Raritan Landing are: 1—Reed canary grass area, 2—Levee bank, 3—Youngest field, 4—Intermediate field, 5—Oldest field, 6—Fencerows and wooded areas and 7—Marsh area.

As fall approaches, the temperature decreases and the hurricane season usually brings heavy rain. Floods, therefore, increase and are longer in duration than those of the summer months. With the opening of the tree canopy in November and lower temperatures, the number of floods increases and they may last longer than one day. The winters are not uniformly cold in this area, so there are periods of thaw which also contribute to the number of winter floods.

Although the average pattern of flooding is a maximum in March and a minimum in June and August, the records show that flooding is very irregular and unpredictable. For example, major floods have been recorded for November 1810, July 1865, September 1882, and October 1903 (Vermeule 1894). A more recent record flood occurred in August 1955 following two successive hurricanes.

FLORA

The species observed on the flood plain of the Raritan River are listed in Figure 7. It is not presumed that this list is all inclusive, but all species predominating in the vegetation are included as well

as numerous others. Nomenclature follows that of Gray's Manual (8th ed. Fernald 1950). Voucher specimens have been deposited in the Chrysler Herbarium at Rutgers University.

One of the most important tree species in flood plain succession is ash. An attempt by the author to separate white ash *(Fraxinus americana)* from red ash or green ash *(F. pennsylvanica)* proved difficult if not impossible with young trees, saplings, and seedlings since fruits having one of the most reliable characters, were generally absent. Proper identification of these species often requires special techniques since there occurs within the genus ecotypic and genotypic variations (Wright 1944a, 1944b, Anderson 1949). The variation found at Raritan Landing made it necessary to lump the species together as *Fraxinus*. Some of the mature trees, however, were definitely identified as *Fraxinus americana* or *F. pennsylvanica*. *Fraxinus* regardless of species will be referred to as ash except where identification was reasonably certain.

AREAS OF DETAILED STUDY

BURNT MILLS

The influence of slight differences in topography on flood plain vegetation is well illustrated near Burnt Mills (Fig. 3). The flood plain at this location was studied critically at several places: a well-developed flood plain with adjacent terrace, river banks of the erosional and depositional types, and two islands along the margin of the river (Fig. 8). The following account of these areas is based upon transect, quadrat and reconnaissance data.

THE FLOOD PLAIN AND TERRACE

Most of the uplands at the Burnt Mills location are or have been used agriculturally. However, below the Somerset Airport there is an especially wide area of woodland extending from the river well on to the upland. The presence of some multi-trunked trees and cattle fences in the woods suggest past cutting, followed by a period of pasturing. Nevertheless, some trees 100 ft tall and some with trunk diameters as great as 38 in. d.b.h. indicate that disturbance had not been severe nor had it been recent. The lower portion of the woods where occasional flooding occurs might generally be designated as a flood plain forest. When studied critically smaller plant communities become apparent.

Near the river there exists one such community, partly cut off from the mainland by a slough which is about 10 m wide and deep enough to retain water during periods of drought. This community will be referred to as the outer flood plain (Fig. 8). Inland from the slough there is a low area which has been dissected by an irregular pattern of shallow sloughs. The community occupying this area will be referred to as the inner flood plain community. Farther inland there is a terrace which is only about 110 m wide which floods on rare occasions, such as the flood of August 1955 (personal communication,

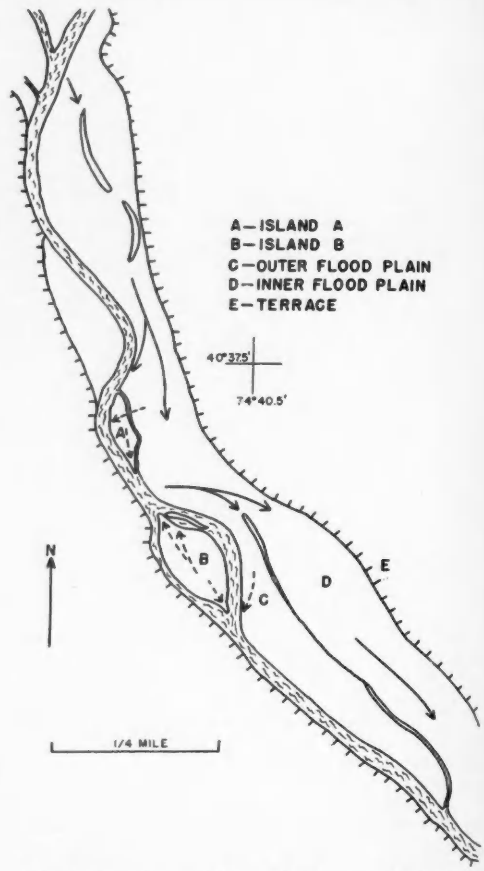

FIG. 8. Detail map of Burnt Mills area showing locations of study areas, the general flooding path in the inner flood plain, and the direction of island growth.

M. F. Buell). The vegetational differences allow the recognition of a third community, the terrace community. These communities are the same as those studied for their woody species composition by Buell & Wistendahl (1955).

From quadrat and line intercept studies Buell & Wistendahl (1955) determined that the forest of the outer flood plain was heterogeneous in tree composition with beech *(Fagus grandifolia)*, sugar maple *(Acer saccharum)*, tuliptree, slippery elm *(Ulmus rubra)*, and basswood *(Tilia americana)* contributing conspicuously to the data. The forest of the inner flood plain was composed of species of trees more characteristic of moist areas: elm, red maple *(Acer rubrum)* and others. The forest of the more mesic terrace suggested a trend toward maple-beech-basswood. In the present study, data from a line transect extending from the river to the upland show differences in the herb, shrub, and tree species composition in each of the three communities and in transitional areas between them.

Variation in species composition of the 3 plant

communities was evident along the transect (Fig. 9). River birch *(Betula nigra)*, ironwood *(Carpinus caroliniana)*, slippery elm and boxelder *(Acer negundo)* appeared only on the outer flood plain, although away from the transect some individuals were found on the inner flood plain. Elsewhere along the edge of the river but not along the transect the same general pattern of tree distribution occurs, except for local dominance of beech or less frequently sycamore *(Platanus occidentalis)*. Several species—American elm, bitternut hickory *(Carya cordiformis)*, tuliptree, ash *(Fraxinus americana)*, and sugar maple were also on the outer flood plain.

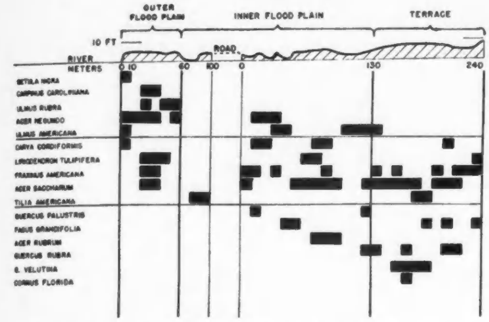

FIG. 9. Distribution of tree species along the transect line extending from the river to above the terrace at Burnt Mills area. Data based on presence of species within 10 m segments of transect. Vertical profile exaggerated about six times.

Throughout much of the inner flood plain there are series of shallow sloughs, most of which are more or less connected with each other forming a network of low areas. These areas vary in width and depth but are all the result of erosion. The species composition of the slough and interslough areas differ. In general, trees do not occur on the slough itself but occupy the interslough areas. Noticeable exceptions are boxelder and river birch which are occasionally in low areas. Trees, undercut by the erosion process, have fallen or are leaning over the sloughs. The general lack of trees in these wet areas has resulted in openings in the canopy. However, trees on the borders shade much of the slough areas.

The interslough areas of the inner flood plain varied greatly in width. One area through which the transect line passed, although only 2 or 3 m wide, supported mature trees. A red oak *(Quercus rubra)* 15.6 in. d.b.h. formed the obstruction which caused an erosion pattern that created two sloughs downstream from it, separated by an uneroded, wedge-shaped interslough below the tree (Fig. 10). Sugar maple, American elm, beech and a large white oak *(Quercus alba)*, 30.1 in. d.b.h., occurred on this interslough area in the vicinity of the transect line. Other interslough areas were much wider—up to 40 m. The vegetation of these wider areas was much more mesophytic and bore some similarity to that of

FIG. 10. Photograph of inner flood plain taken March 1955 looking "upstream." Wedge shaped interslough was formed by the deflection of flood water by red oak at the point.

the outer flood plain and the terrace. On the entire inner flood plain, including the sloughs and intersloughs, there were 17 tree species; 13 species occurred along the transect and among these were mature individuals of tuliptree, bitternut hickory, basswood, beech, elm, red maple, pin oak *(Quercus palustris)*, white oak and red oak.

On the terrace, the highest and best drained habitat, sugar maple, although not the largest tree, contributed the most cover. It also had the greatest tree density, sapling cover, and seedling density (Table 2, also Buell & Wistendahl 1955). Associated with the sugar maple were tree species which indicate a difference in conditions here as compared to the outer flood plain and the lower, wetter, inner flood plain. Black oak *(Quercus velutina)* for example, present only on the terrace, was quite abundant and attained sizes as great as 19.8 in. d.b.h. Red oak and flowering dogwood *(Cornus florida)* were also found in greater abundance than anywhere else. Missing were the boxelder, river birch, and occasional black gum *(Nyssa sylvatica)* of the lower areas.

Seven species of shrubs and lianas were present on the outer flood plain of which spicebush *(Lindera benzoin)* had the highest cover value along the transect. This species was also common on the inner flood plain. Saplings of sugar maple occupied the better drained interslough areas and contributed heavily to the shrub-sapling cover values. Over considerable stretches along the transect, shrubs were sparse especially on the terrace.

Slight undulations of topography on the outer flood plain influenced the distribution of the herbaceous species. Viola, *Alliaria officinalis*, and *Impatiens capensis* were abundant in the moist, shaded areas. *Aster divaricatus* was common on the higher ground. The outer flood plain had many species in common with the inner flood plain but few in common with the terrace.

The deep slough between the outer and inner flood plain is pond-like most of the year and has flowing water only during floods. The eroding action of floods has undercut trees on the inner or main-

land bank exposing their roots and causing some trees to lean or fall across the slough. The bank on the outer flood plain side is less steep, as some soil from the outer flood plain has been washed into the slough. Both banks, except where erosion is severe, support a rich mixture of plants with large stands of *Impatiens capensis,* some heavily infested with Cuscuta, masses of *Boehmeria cylindrica, Pilea pumila, Panicum clandestinum* and *Myosotis scorpioides.* An occasional stand of *Lobelia cardinalis* adds color to the area. In the water one may find *Nuphar advena,* Myriophyllum, Potamogeton, and an almost complete cover of *Lemna minor,* depending upon the location and time of the year. The water is rich in algae.

Although 43 species of herbs were recorded along the transect which extended across the inner flood plain, and despite the fact that there are many more than that number in the area, single species often dominated parts of the sloughs. *Glyceria septentrionalis* and *G. striata* covered large areas in early summer, and in other parts of the same slough, *Myosotis scorpioides* grew in profusion. Other species which were conspicuous are listed in Figure 7.

As a result of the low terrain and the shading by trees, the slough areas remain moist for most of the year. Only during the dry summer months do some of them become free of standing water. In winter they are almost all wet and are often frozen over. The soil in the sloughs is rather heavy with clay and is mottled at a depth of 6 to 8 in. The herbaceous vegetation develops after the sloughs dry out; thus they become vegetated at a later date than the better drained places between them. A sodden layer of litter frequently covers large areas with little or no vegetation even as late as June. However, with the reduction in soil moisture during the summer months, the parts of these areas which receive adequate sunlight become covered with plant life, even though shaded portions remain sparsely vegetated.

The composition of the herbaceous layer on the terrace was very different from any of the other areas. Very few herbs were present in July. In early summer *Podophyllum peltatum* was common but by late June it had largely died back to the ground. There were only 19 species of herbs along the transect on the terrace as compared to 43 on the inner flood plain.

Between the terrace and the upland there was a low area which bore some similarity to the sloughs except that it was higher and above the flood level. The vegetation was very similar to that of the low sloughs but had a greater cover of herbs. *Glyceria septentrionalis* was dominant locally and there was an abundance of mosses.

In the present study data for early summer herbaceous species (Table 1) and tree seedlings (Table 2) were obtained from quadrats during the period May 28 to June 10, 1954. Two months later, August 27 to September 4, the late summer herbaceous growth and the changes that had occurred during the intervening months were recorded.

There were 63 species of herbs recorded on quadrats at the three locations during the entire summer. More kinds of herbs were present on the outer flood plain and on the inner flood plain than on the terrace. The amount of herbaceous cover was greater in early summer than in late summer at each of the 3 locations. *Mertensia virginica,* which was dying back at the time the early summer data were obtained, had the highest cover value, 7% on the outer flood plain. *Impatiens capensis* had the highest cover value, 33% on the inner flood plain and *Podophyllum peltatum* the highest, 53%, on the terrace. By late summer the species composition had changed resulting in a striking difference in the percentage of cover of the various species. On the outer flood plain Mertensia was no longer in the active state of growth and *Aster divaricatus* had the highest cover value, 9%. *Leersia oryzoides* and *Boehmeria cylindrica* contributed the most cover on the inner flood plain with 13% and 9% cover respectively. No single herb species had a cover value greater than 1% on the terrace; however, sugar maple seedlings grew in profusion and covered most of the ground.

Differences in the number and kinds of tree seedlings were found in each of the 3 communities (Table 2). On the outer flood plain in early summer there were only 24 seedlings per 40 sq m; whereas, on the terrace there were 423 seedlings for the same area. Correspondingly, only 2 species of seedlings were present on the outer flood plain quadrats and 9 were found on the terrace quadrats. Sugar maple seedlings were most abundant in these 2 communities. They occurred with 79% frequency on the terrace but only 20% on the outer flood plain. On the inner flood plain seedlings of boxelder were the most numerous.

Data obtained in late summer from the same communities indicated an increase in the number and species of seedlings (Table 2). Three more species appeared on the outer flood plain, and the total number of tree species as seedlings increased from 24 to 31. On the terrace the same number of species were present as in the early summer, but there was an increase in the total seedling count. Red maple and tuliptree seedlings were abundant on the inner flood plain where they had been absent in early summer.

RIVER BANKS

There are two kinds of river banks at Burnt Mills: (1) those where transported materials are being deposited and (2) those where the eroding action of the river has undercut the banks. Where deposition occurred, the soil is gravelly with an intermixture of sand and little silt. These areas are immediately and often deeply inundated during floods but during dry periods are exposed and have a rich cover of herbaceous plants. Tree species on the areas of deposition are sycamore, river birch, boxelder, American elm, and slippery elm. Shrubs are not very common on the

TABLE 1. Percent cover (C) and % frequency (F) of herbaceous species on quadrats at three locations—outer flood plain (OFP), inner flood plain (IFP), and terrace (Ter.)—in the Burnt Mills area and in Mertensia Woods during early and late summer. D—Density, F—Frequency, X—cover values less than 1%.

	Burnt Mills												Mertensia			
	Early Summer						Late Summer						E. Sum.		L. Sum.	
	OFP		IFP		Ter.		OFP		IFP		Ter.		Woods		Woods	
	% C	% F	% C	% F	% C	% F	% C	% F	% C	% F	% C	% F	% C	% F	% C	% F
Acalypha virginica									X	8						
Agrostis tenuis											X	3				
Alliaria officinalis	3	60					3	48								
Allium tricoccum					X	3	X	3					1	60	1	48
A. vineale	X	28	X	15									X	10		
Amphicarpa bracteata			X	8					X	13						
Arisaema triphyllum	1	5	2	50	X	10	X	5					X	5		
Asarum canadense							X	3								
Aster divaricatus	6	63	2	23	X	3	9	73	1	23	X	3				
A. simplex									X	5						
Boehmeria cylindrica			1	8					9	25						
Carex amphibola	X	20	1	25	X	3	X	10	1	8	X	5			X	3
C. grayii	X	3	X	8			X	10	1	25	X	3			X	8
C. lupulina			2	13												
C. rosea	X	5	X	8	X	13			1	28	X	5	X	3	X	8
Caulophyllum thalictroides													10	25	2	10
Cinna arundinacea							X	23	X	8					X	10
Circaea quadrisulcata	X	5	4	25	6	48	1	13	1	25	X	43				
Commelina communis									X	3						
Cryptotaenia canadensis	X	8	X	3			X	3	X	3			X	13	X	3
Dentaria laciniata	X	10	X	3	X	3							X	5		
Echinocystis lobata															X	3
Floerkea proserpinacoides	X	3														
Galium sp.	X	3	X	3	X	3			X	3	X	3	X	15		
Geranium maculatum	1	33			X	13	X	20								
Geum canadense	X	8	1	28			X	25	X	25			X	3	X	15
Glyceria septentrionalis									X	5						
G. striata			1	3			X	3	X	5						
Hydrophyllum virginianum	2	43	X	3			X	13					11	72	5	80
Hystrix patula					X	3										
Impatiens capensis	3	43	33	83	2	40							1	26		
Laportea canadensis	X	8	X	3			X	8	X	3			42	88	27	78
Leersia oryzoides							X	3	13	63			X	6	X	3
Lycopus virginicus			X	15					1	10						
Lysimachia nummularia			2	23												
Mertensia virginica	7	83														
Myosotis scorpioides							X	3								
Osmorhiza claytoni	X	3	X	3	X	3										
Oxalis sp.	X	3	X	3	X	3	X	3	X	3						
Panicum clandestinum	X	3					X	3								
Pilea pumila							X	3	1	28						
Poa pratensis	X	5	X	13	X	28			X	3	X	28	X	13	X	3
Podophyllum peltatum	4	23	8	35	53	100							1	8		
Polygonatum biflorum	X	10							X	3			X	13		
P. canaliculatum													X	3		
Polygonum arifolium									X	3						
P. hydropiper			X	3					X	20						
P. pensylvanicum			X	10					X	25						
P. sagittatum			X	3					X	3						
Potentilla canadensis	X	3	X	3			X	3	X	8						
Ranunculus abortivus	X	3	X	5												
Rudbeckia laciniata							X	3								
Sanguinaria canadensis					X	20							X	3		
Sanicula gregaria	X	10											1	25	X	13
Scutellaria lateriflora									X	8						
Sicyos angulatus							X	3								
Smilacina racemosa			X	3	X	3					X	3				
Solidago caesia (?)			X	10	X	3										
S. flexicaulis	X	5					1	15					5	52	5	45
S. rugosa							X	3			X	5				
Thalictrum sp.							X	3								
Tovara virginiana	1	15					1	28	X	10			1	15	2	18
Viola spp.	4	53	1	13	1	48	2	48	X	3			3	40	3	30
Botrychium sp.											X	3				

TABLE 1. (Continued)

	Burnt Mills												Mertensia			
	Early Summer						Late Summer						E. Sum.		L. Sum.	
	OFP		IFP		Ter.		OFP		IFP		Ter.		Woods		Woods	
	% C	% F	% C	% F	% C	% F	% C	% F	% C	% F	% C	% F	% C	% F	% C	% F
Mosses	1	25	1	30	X	3	X	30	X	28	X	3	2	35	1	25
Logs	5	35	4	25	1	13	3	15	2	18	2	23	2	8	1	25
Litter cover	77	100	98	100	95	100	59	100	77	100	86	100	57	100	19	98
Litter depth (cm)	1.8		1.8		2.2		1.1		1.2		1.4		0.9		0.5	
SPACE	58	100	45	98	29	100	82	100	68	95	97	100	26	75	53	100

TABLE 2. Number of tree seedlings on 40 quadrats (0.5 x 2 m) on 3 locations—outer flood plain (OFP), inner flood plain (IFP), and terrace (Ter.)—in the Burnt Mills area and in Mertensia Woods during early and late summer. D—Density, F—Frequency.

	Burnt Mills												Mertensia			
	Early Summer						Late Summer						E. Sum.		L. Sum.	
	OFP		IFP		Ter.		OFP		IFP		Ter.		Woods		Woods	
	% D	% F	% D	% F	% D	% F	% D	% F	% D	% F	% D	% F	% D	% F	% D	% F
Acer saccharum	19	20	3	8	358	77	18	15	2	5	410	70				
A. negundo	5	8	8	8	13	25	5	10	12	15	8	18	13	15	6	10
Carya cordiformis			3	8	7	18	2	5	4	10	8	18				
Cornus florida			1	3	7	5					1	3				
Fraxinus americana			2	5			5	8	1	3	2	5				
Quercus palustris			2	5					1	3						
Ulmus americana					33	33	1	3			32	33			1	3
Prunus serotina					2	3										
Quercus velutina					1	3					3	8				
Q. rubra					1	3					2	10				
Carpinus caroliniana					1	3										
Crataegus sp.									2	5						
Acer rubrum									19	10						
Liriodendron tulipifera									13	8						
Tilia americana (sprouts)											2	3				
Number of species	2		6		9		5		8		9		1		2	
Total seedlings	24		19		423		31		64		466		13		7	

newly deposited areas. Spice bush is one of the first to appear, but only after trees have grown enough to produce some shade.

There was no clear evidence of vegetational zonation on these usually small areas of deposition, but a change was evident in the vegetation from the river inward. On the edge of the river the trees were younger than those farther in. River birch and sycamore commonly formed clusters of young sprouts near the water. Shrubs and seedlings were usually absent, but during the summer months there was a profusion of herbs. Growing in the shallow water at the edge of the banks were *Elodea canadensis, Ludwigia palustris, Lindernia dubia,* and occasionally some Potamogeton. On the very edge of the water, masses of *Polygonum hydropiper* were very common. Many species of *Polygonum* were found on these areas of deposition including: *P. pensylvanicum, P. coccincum, P. sagittatum, P. scandens, P. lapathifolium, P. arifolium* as well as *Tovara virginiana.* In addition, 32 other herbs were found on one area of deposition which was about 100 sq m in size. Of these *Pilea pumila, Poa pratensis, Verbena urticifolia, Oxalis europaea, Panicum clandestinum, Carex stricta,* and *Impatiens capensis* were abundant.

ISLAND

One of the largest islands in the Burnt Mills area (island B, Fig. 8), 380 m long, was studied by means of transect and reconnaissance. Data along a single transect which extended the full length of the island were obtained during the period July 7th to July 20th, 1954. This island had been greatly disturbed in the central part where, at the time of sampling, soil was being trucked out. In summer, when river flow was low, there was little or no water flowing over the 10 to 20 m wide river bed of red shale which lies along the western side of the island. The main course of the river lies on the eastern side of the island and flows over a bed of coarse gravel. Topo-

graphically the island was highest near the center (about 4-5 ft above the river) and more or less low and wet near the margins. The upper end of the island from the beginning of the transect to 110 m was low, uneven and subjected to most frequent flooding (Fig. 11). The middle portion of the transect extended from 110 m to 240 m and traversed the high central section of the island which was level and infrequently flooded. The last section of the transect from 240 m to 380 m traversed the lower part of the island whose surface was uneven. This section was lower than the middle but not as low as the upper end. The lower tip of the island, the last 4 m, was a sandy point exposed only during low water. Dense vegetation, especially the herb layer, covered the island.

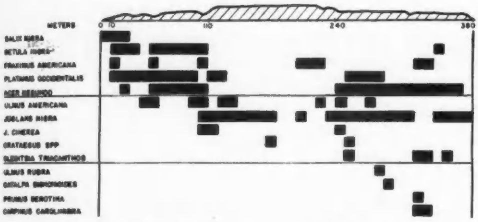

FIG. 11. Distribution of tree species along a single transect line extending the full length of an island, island B, in the Burnt Mills area (Fig. 8). The transect starts at the upstream end of the island at 0 meters. Data based on the presence of species within 10 m segments of transect. Vertical profile exaggerated.

From the upper to the lower end of the transect there was a transition in the saplings and trees (Fig. 11). The surface for the first 110 m gradually increased from water level to a height of about 1 m above the river. In this section there were many sloughs and a large accumulation of logs and flood debris. Black willow *(Salix nigra)* saplings were numerous as a result of sprout growth and were the first woody plants along the transect and only along the first 30 m. River birch first appeared along the second 10 m segment of the line and was the first tree species with stem diameters greater than 1 in. d.b.h. This species was represented on the transect for a distance of 110 m. Stem diameters increased along the transect from 2.2 in. at about 20 m to 11.8 in. at about 70 m, after which most stems were greater than 6 in. Associated with the river birch were several other species, predominantly sycamore, forming masses of sprout growth with stems mostly over 1 in. d.b.h. This species occurred as far as 130 m from the upper end and in places completely shaded the ground. A tree with a d.b.h. of 21.5 in. was encountered about 120 m from the upper end, while the first one at about 30 m was only 1.8 in. d.b.h. Boxelder, mostly as saplings or sprouts, was also represented at the upper end; its greatest contribution to cover being between 50 and 110 m from the end of the island. Other trees present on the first 110 m were ash, American elm, silver maple *(Acer saccharinum)*, black walnut *(Juglans nigra)*, and butternut *(J. cinerea)*. The latter two species were only on higher ground and were the most important trees on the higher central area. Silver maple was not as common as were elm and ash, which were general throughout the island.

Although the sprout growth of willow, river birch, sycamore, and boxelder gave a shrubby appearance to the upper end of the island, few shrubs or lianas were present. Only speckled alder *(Alnus rugosa)*, silky dogwood *(Cornus amomum)*, and poison ivy *(Rhus radicans)* were found along that part of the transect.

Herbs were very abundant on the island, and 84 species were identified along the entire 380 m of the transect (Fig. 7). Unoccupied space rarely amounted to 70% along the line except where there was an accumulation of flood deposited debris or where there were sloughs too wet to support vegetation. During periods of low river flow, herbs were present on the exposed gravelly river bed on the upper end of the island. Herb cover there was not complete but was represented by a large number of rather widely spaced individuals. The species that were on the open, gravelly bed at the upper end of the island made up most of the herbaceous vegetation for the first 110 m of transect. After that distance the topography rose rather abruptly from a slough to the high central portion.

The tree cover of the central area was rather open. One 30 m section of the transect had no tree cover at all. Black walnut and butternut were common, although many other species were present, including elm, ash, shagbark hickory *(Carya ovata)*, and hawthorn *(Crataegus)*. Although shrubs and lianas were more common on this middle portion of the island, they were not frequent and consisted mostly of blackberry *(Rubus)* and grape *(Vitis)*. The herbs *Alliaria officinalis* and *Impatiens capensis* were extensive on the slope from the low area. On the higher central ground goldenrods of several species were frequently dominant with an underlying cover of grasses and sedges, particularly *Agrostis tenuis* and *Carex rosea*. Locally along the line *Panicum clandestinum, Teucrium canadense, Lysimachia nummularia, Helianthus decapetalus, Silphium perfoliatum, Geum canadense, Glechoma hederacea*, and *Laportea canadensis* were abundant.

The lower end of the island had more kinds of trees than the upper end; boxelder was one of the most abundant. River birch and sycamore were represented on the lower end but only near sloughs. Hawthorn, slippery elm, catalpa *(Catalpa bignonioides)*, black cherry *(Prunus serotina)*, and ironwood were also present. On the lower end shrubs and lianas were more abundant. Spicebush and blackberry were most frequent and were dense locally. Found occasionally were grape, honeysuckle *(Lonicera japonica)*, and elderberry *(Sambucus canadensis)*. On the lower end of the island where tree, sapling, and shrub cover was greatest, there was least

herbaceous cover. The extreme lower end of the island dropped off suddenly where at low water a low, sandy point extended 4 m to the river. Here *Teucrium canadense* and *Verbena urticifolia* gave way to *Leersia oryzoides* dominance at the edge of the water.

Although trees were rather small on the island, mostly 6 to 8 in. d.b.h., one sycamore on the lower end measured 55.0 in. d.b.h. The largest American elm was 25.6 in. d.b.h.; white ash, 29.1 in. d.b.h. Seedlings were rare, and only 3 species were encountered at sampling places along the transect, boxelder, silver maple, and pin oak, with totals of 3, 12, and 1 respectively.

Upstream from island B there was another rather large island, island A, which was about 250 m long and 50 m wide (Fig. 8). Diameter measurements of several of the largest of the most common trees near the center of the island showed the following: pin oak, 27.2, 28.2; shagbark hickory, 19.7, 18.5, 15.4; white ash, 17.5, 17.0; hackberry, 23.5, 10.9; boxelder, 13.8; American elm, 12.2; slippery elm, 5.0 in. These were the most important species, which formed an almost completely closed canopy. They varied greatly in size. Few saplings were evident except for those of boxelder which grew in abundance, especially along the edges of the island and along sloughs. The shrub layer consisted largely of spicebush, which covered about 50% or more of the island. Some bladdernut *(Staphylea trifolia)* and barberry *(Berberis thunbergii)* were also present in minor amounts. On the periphery of the island, especially on the upper end, poison ivy was profuse. Species found in sloughs and other habitats in the Burnt Mills area are listed in Figure 7.

MERTENSIA WOODS

On the rather extensive flood plain below the confluence of the North and South Branches of the Raritan River, there is a small but relatively undisturbed wooded area which physiographically is similar to the outer flood plain at the Burnt Mills study area (Fig. 12). It is partially cut off from the main part of the flood plain by a deep slough and has been referred to by local botanists as Mertensia "island" because of the profusion of *Mertensia virginica*. It is referred to as Mertensia Woods in this paper. This area was the subject of detailed study using quadrat and transect methods similar to those of the Burnt Mills studies.

A detailed study of the woody species of this area was made by Buell & Wistendahl (1955). Eleven tree species were found along cover transects and of these slippery elm and hackberry were the dominants. About 10% unoccupied space occurred in the tree canopy. Diameters at breast height of some of the largest trees were: slippery elm 34.2, 17.5, 15.6; hackberry 40.8, 28.0, 27.0; black walnut 34.9, 20.0, 17.0; and ash 22.7, 20.0, 16.5 in. Few large sugar maple, pin oak, and shagbark hickory trees occurred on this area. Although trees were of various sizes.

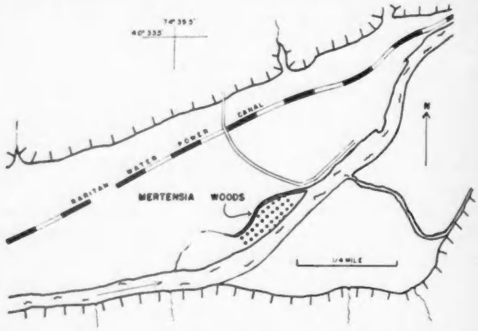

FIG. 12. Map of flood plain near Raritan, N. J., showing location of Mertensia Woods in which detail studies (dotted area) were made. This is location "B" on Fig. 1.

saplings were not abundant. At the sapling-shrub level bladdernut and spicebush were the dominant shrubs and in places formed an almost completely closed layer.

The species forming the herb cover in early summer, June 15, 1954, and in late summer, September 8, 1954, are presented in Table 1. The June date was too late to record any of the typical spring flowering plants, such as *Mertensia virginica, Claytonia virginica,* and Viola, which were present in early May. Differences in the herbaceous cover between seasons were not as striking at Mertensia Woods as at Burnt Mills—22 species of herbs in early summer and only 17 in late summer. Six species had cover values greater than 1% in early summer—*Laportea canadensis* 42%, *Hydrophyllum virginianum* 11%, *Caulophyllum thalictroides* 10%, *Solidago flexicaulis* 5%, and Viola 3%. The cover values for the first 3 species decreased by late summer to 27, 5, and 2% respectively. The last two species had no change in cover. *Tovara virginiana,* which had only 1% cover in early summer, was the only species to show an increase in value by late summer. None of these 6 species was missing at the late summer date. The amount of unoccupied space in the herb layer for late summer amounted to 53%, which was about twice the value of early summer.

There was no noticeable tree reproduction in the well developed part of the woods, although quadrat studies in early summer showed 13 boxelder seedlings on 40 sq m (15% frequency). In late summer only 6 boxelder seedlings and one American elm seedling were recorded on the quadrats. This general paucity of seedlings also characterized the outer flood plain at Burnt Mills.

Litter covered 57% of the ground in early summer. By late summer the value had decreased to 19%. Somewhat comparable figures were obtained on the outer flood plain at Burnt Mills (Table 1). This decrease occurred in spite of the fact that no flooding of the area took place between sampling dates.

A transect from the edge of the river across the woods showed a striking transition in the topography

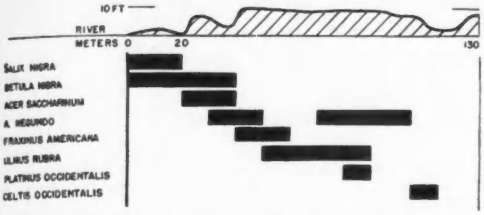

FIG. 13. Distribution of species along a single transect extending from the river across the natural levee or outer flood plain which is occupied by Mertensia Woods. Data based on presence of specimens within 10 m segments of the transect. Vertical profile exaggerated about 3 times. Horizontal distance is given in meters, vertical in feet.

and the associated vegetation (Fig. 13). Starting at the river, the first trees were black willow, which formed a dense cover on a small sandy deposit. The next trees were river birch. On a larger and higher sand bar farther in from the river silver maple assumed dominance and overtopped the smaller river birch. Continuing in from the river, boxelder and ash became important, and willow, river birch, and silver maple successively lost dominance.

Along the transect, shrubs were sparse for the first 30 m from the river. After that, spicebush formed a dense cover. Occasionally bladdernut was found in abundance. Small amounts of poison ivy and Virginia creeper (*Parthenocissus quinquefolia*) were present.

Herbs were variously distributed along the transect. At the edge of the river there were 19 species with Polygonum contributing the most cover. Herbs were under the dense cover of willows, but were more important in and around the sloughs between the low sand bars. The first slough encountered was predominantly covered with *Phalaris arundinacea*. *Ludwigia palustris* occupied much of the wetter spots. In the second slough *Carex grayii*, Viola, *Impatiens capensis*, and *Geum canadense* were common. From the second slough back across the woods *Laportea canadensis* was dominant (50% cover). Viola, *Alliaria officinalis*, and *Impatiens capensis* were less abundant, along with several other species. The deep slough behind the woods had almost 100% herb cover of which *Phalaris arundinacea*, *Polygonum arifolium*, *Peltandra virginica*, *Impatiens capensis*, *I. pallida*, *Hystrix patula*, *Myosotis scorpioides*, *Sparganium americanum*, Cuscuta, *Laportea canadensis*, and *Geum canadense* were most conspicuous. Additional species for all these areas are listed in Figure 7.

DISCUSSION OF BURNT MILLS AND MERTENSIA WOODS AREAS

Detailed studies of the vegetation in the Burnt Mills and Mertensia Woods areas show that slight differences in topography and flooding effects have a marked influence on vegetation, and that flood plain dynamics can be interpreted from the topography and vegetation. River banks, islands, sloughs, and vegetation are all useful in interpreting the changes that are taking place in the course of the river.

Old meander patterns are especially discernible on air photos of the Burnt Mills area, and it is likely that flood plain formation and destruction throughout the river system has occurred many times in the past. The present vegetation where it is best developed reflects not only the potentialities of the mature forest but also shows the general pattern of construction and destruction of the river flood plain.

The topography and the vegetation of island A at Burnt Mills show that there is a tendency for this island to build out toward the main channel of the river and that the slough on the east side of the island is filling up (Fig. 8.) Downstream, island B, on the other hand, is building at its upper end and toward the main channel where small subsidiary islands have developed. The upstream migration of island B will probably not be great, as the usual tendency is for islands and meander patterns to move downstream (Cowles 1901, Turner 1931, Matthes 1941). Braun (1916) found islands near the margin of the Little Miami River in Ohio which seemed to be growing toward the main channel rather than downstream. Both islands, A and B, at Burnt Mills showed somewhat similar development, although the small adjacent islands showed the characteristic downstream growth Island B will continue to grow toward the main channel as long as the river meanders farther to the east at that point. The eastward meander is also made evident by active undercutting of the outer flood plain across from island B. Further evidence of eastward meander is found on the inner flood plain (Fig. 8, D). Here single erosion sloughs are often divided into two by mature trees which have prevented erosion below them (Fig. 10). The severity of erosion on the inner flood plain as compared with the outer flood plain indicates that at times of major floods much of the force of the river is diverted by the meander into this inner flood plain.

The well developed forests of the Burnt Mills and Mertensia Woods flood plains are indicative of the mesophytic forests that probably once occupied much of the natural levees along the Raritan River and which could possibly once again exist if allowed to develop fully (Buell & Wistendahl 1955). The development of mesophytic forests on flood plains has been described by Cowles (1901), Nichols (1916), Braun (1916), and others for other flood plains in the deciduous forest regions. The successional trend is toward mesophytic conditions, which may later be destroyed by the meandering river. Mertensia Woods, like that on the outer flood plain at Burnt Mills, is composed of mature trees of a mixture of species. Deposition is active in Mertensia Woods and the forest will tend to occupy a wider area as the sand bars adjacent to it become more mesic. On the other hand, the outer flood plain at Burnt Mills is being eroded away and some of the magnificent trees now occupying that area stand close to the undercut

river bank. That the two areas are not identical in their tree composition is not surprising, considering the differences in location, use, and stream action.

RARITAN LANDING

The section of the flood plain extending about 1 mi. upstream from Landing Lane (Fig. 14), subjected in the past to various land uses, now supports a variety of plant communities. With its natural

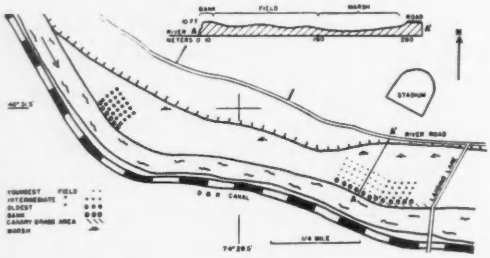

FIG. 14. Map of Raritan Landing area showing location of study areas. Vertical scale of profile A—A′ exaggerated 6 times.

levee next to the river and marshland behind, the flood plain presents striking soil variations (Fig. 2). Of all the flood plain sites, the margin of the levee nearest the river has been least disturbed and has a large number of trees of different sizes and species. The poorly drained marshlands behind the levee are dominated by grasses, sedges, and other plants characteristic of wet places. The better drained soil of the levee itself was for the most part cleared of its original plant cover but is now in various stages of revegetation. To discover the characteristics of the vegetation of these closely associated habitats, detailed studies were made of several rather distinct plant communities.

The lowlands along the Raritan River have a long history of utilization. Prior to the coming of the white man the Raritang Indians cultivated the fertile bottom lands (Walsh 1928). The earliest land grant for the north bank of the river (Raritan Landing) lying opposite New Brunswick dates back to 1685 (Vermeule 1936). According to Vermeule, dams and mills functioned in the Landing Lane area from 1750 to 1833 when the Delaware-Raritan Canal was constructed along the south bank. Wharves and warehouses prospered at Landing Lane until floods and changing economy destroyed them. By 1875 all the warehouses were destroyed and ". . . the green grass grew and cattle grazed over the site of Raritan Landing." (Vermeule 1936).

REVEGETATION OF FIELDS

Aerial photographs taken in 1940 of the Landing Lane section of Raritan Landing show several distinct fields varying in size and bordered by hedgerows. Some fields on the slopes adjacent to the flood plain were under cultivation. Those of the flood plain, however, had ceased to be used agriculturally. These fields, abandoned at different dates, are readily discernible as one traverses the mile-long section.

Three fields which were abandoned at different dates but which were on similar soil were studied in detail (Fig. 14). The largest of the three fields was about 3 A and had been used most recently for agriculture. This field will be referred to as the youngest field. The exact date of abandonment is unknown; however, an ash sapling 6 ft tall had 7 growth rings at its base. Although a few red cedars (*Juniperus virginiana*) were as tall as 12 ft, the average was about 8 ft; one 8 ft tree had a ring count of 8. Thus it is obvious that the field was treeless at least 8 years ago, although some seedlings and saplings were undoubtedly present. This youngest field was bordered by river bank vegetation on one side and marsh on the opposite. The other two sides of it had hedgerows of trees.

A second field (the intermediate field) had ash trees with ring counts at breast height up to 16. Allowing 5 yrs for a tree to grow to 4.5 ft, one would presume that it has probably been at least 21 yrs since this field was treeless.

A third field had ash trees with ring counts up to 31 at breast height. Using the same basis as above, this field was treeless about 36 yrs ago and will be referred to as the oldest field.

The soils of these 3 adjacent fields are similar, since they occupy the same relative position on the top of the natural levee. The great variation in soils occurs as one goes from the river toward the upland. The characteristics of this levee soil were obtained in a soil transect study that transversed the youngest field (Fig. 2).

A comparison of the data for the herbaceous vegetation found on quadrats on the 3 fields presents some striking differences. A total of 70 species of herbs contributed to cover on all 3 fields, with only 5 species common to all fields (Table 3). Unoccupied space for the youngest field was only 7%, whereas it was 47% and 81% for the intermediate and the oldest field respectively.

On the youngest field *Agrostis tenuis* contributed 55% cover. This species occurred with almost 100% frequency and dominated the field with respect to cover (Table 3). *Solidago graminifolia, Panicum clandestinum, Andropogon scoparius,* and *Solidago canadensis* contributed conspicuously to cover through the matrix of Agrostis. On the intermediate field Agrostis contributed 48% cover and on the oldest field less than 1% cover.

On the oldest field the only species contributing more than 3% cover was *Carex rosea,* 11%. There were 29 other herbaceous species. Most of them do not appear in the data for the other two fields. Heliophytes were poorly represented, whereas shade tolerant species, such as *Alliaria officinalis, Geranium maculatum,* and Viola were more abundant. The total cover contributed by herbs amounted to 19%, which was 74% less than the youngest field and 34% less than the intermediate. As the flood plain becomes a young woodland, there is a change in the

TABLE 3. Percent cover (C) and % frequency (F) of herbs on 3 fields at Raritan Landing. Based on 80 quadrats (0.5 x 2 m) for the youngest field and 40 quadrats (0.5 x 2 m) for the intermediate and the oldest field. X—less than 1% cover.

Species	Youngest		Intermediate		Oldest	
	% C	% F	% C	% F	% C	% F
Agrostis tenuis	55	94	48	88	X	3
Solidago graminifolia	15	86	X	3		
Panicum clandestinum	10	58	X	6	X	10
Solidago canadensis	7	39	X	3		
Andropogon scoparius	4	34	X	3		
Potentilla canadensis	3	43	3	53	1	43
Achillea millefolium	2	85	2	20		
Pycnanthemum virginianum	X	54	X	3		
Solidago gigantea	X	20	X	10		
S. nemoralis	X	16	2	48		
Oxalis europaea	X	29	X	50	X	10
Apocynum cannabinum	X	13	X	8		
Aster lateriflorus	X	13	X	3	1	13
A. ericoides	X	11	X	10		
Solidago juncea	X	10	2	28		
Aster novae angliae	X	9	X	40		
Triodia flava	X	7	3	30		
Allium vineale	X	6				
Physalis heterophylla	X	4				
Bidens coronata	X	4	X	5		
Panicum virgatum	X	3				
Solanum carolinense	X	3				
Linaria vulgaris	X	3				
Daucus carota	X	3				
Scutellaria integrifolia	X	1	X	3		
Erectites hieracifolia	X	1				
Acalypha virginica	X	1	X	3		
Trifolim agrarium	X	1				
Ambrosia artemisiifolia	X	1	X	18		
Cirsium discolor	X	1	X	5		
Pycnanthemum muticum	X	1				
Thalictrum polygamum	X	1				
Epilobium angustrifolium	X	1				
Geum canadense			X	3		
Oenothera sp.			X	10		
Anthoxanthum odoratum			X	13		
Helianthus decapetalus			X	3	X	5
Fragaria virginiana			X	3	X	23
Polygonum scandens			X	3		
Prunella vulgaris			X	6		
Desmodium paniculatum			X	33		
Lysimachia nummularia			X	5		
Lactuca canadensis			X	5		
Agrimonia parviflora			X	3	X	3
Asparagus officinalis			X	3		
Plantago lanceolata			X	15		
Carex rosea			X	3	11	75
Aster divaricatus					X	25
Galium triflorum					X	30
Carex amphibola					X	30
Hypericum punctatum					X	6
Polygonum pensylvanicum					X	3
Alliaria officinalis					X	35
Lycopus virginicus					X	3
Muhlenbergia tenuiflora					X	15
Geranium maculatum					X	13
Cinna arundinacea					1	10
Tovara virginiana					X	5
Cryptotaenia canadensis					X	5
Viola					1	5
Rudbeckia laciniata					X	3
Eupatorium fistulosum (?)					X	3
Amphicarpa bracteata					X	5
Sanicula gregaria					X	3
Mentha arvensis					X	3
Polygonatum biflorum					X	3
Smilax rotundifolia					X	13
Botrychium					X	30
Mosses					1	48
Space	7	61	47	93	81	96
Number of species. 70	33		35		31	

species represented and a reduction in the amount of ground covered by herbs.

Quantitative data for the woody species growing on these 3 fields were obtained from the transect lines giving cover (Fig. 15) and from quadrats giving density, frequency, and basal area. The species list derived from all sampling included 37 woody species, of which 24 were trees. Sycamore, black walnut, and tree-of-heaven were present on the periphery of some fields but do not appear in the data. Shrubs *(Viburnum acerifolium, Rosa multiflora, Pyrus angustifolia,* and spice bush) were also present but are not represented in the data. Several tree species—ash, red cedar, black cherry, apple *(Pyrus malus)*, elm, hawthorn, and silver maple—were common to all 3 fields, as were the shrubs—poison ivy, silky dogwood, Japanese honeysuckle, grape, blackberry, and black haw *(Viburnum prunifolium)*.

The total of all openings in the tree canopy is referred to as space in Figure 15. On the youngest field, space unoccupied by trees amounted to 99% of the total transect length. Only 3 species contributed to tree cover on this transect—wild black cherry with 80% of the total tree cover, red cedar 17%, and ash 3%. Several other species, such as American elm, red maple, silver maple, pin oak, and hawthorn, were present on the field but did not occur on the transect lines. There were 5 species of trees in the 1.0 to 3.9 in. size class, which was the largest size class represented. American elm and pin oak, absent from transects, were present on quadrats as young trees along with wild black cherry, red cedar, and ash. The density of saplings was greater for ash and elm than for any of the other species. Seedlings were not frequent. Although seedlings of the above 5 species were seen on the field, only elm and wild black cherry seedlings were found on quadrats. The youngest field thus had few tree species greater than 1 in. d.b.h., and these contributed very little cover. Saplings were the most abundant size class of tree species on quadrats, and reproduction although not profuse was evident.

The intermediate field had 60% of the transect lines unoccupied by tree cover. Seven species of

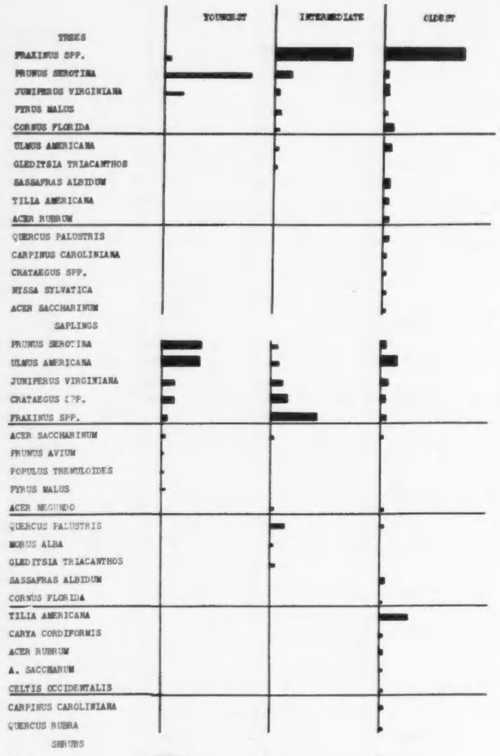

FIG. 15. Percent relative cover and frequency of trees, saplings, and shrubs found along transect lines on three fields at Raritan Landing. Data based on 400 m of transect for the youngest field, 200 m for the intermediate field, and 200 m for the oldest field. Values for less than 3% cover and 20% frequency are represented by a bar the size of that for *Gleditsia triacanthos* tree cover on the intermediate field. Length of bar indicates % cover; width indicates % frequency. For example, on the oldest field Fraxinus had 77% cover with 100% frequency.

trees had representatives over 1 in. d.b.h. and as such were considered contributing to the tree cover. Ash occurred with 100% frequency and contributed 69% cover, whereas the comparable cover values were 17% for black cherry and 5% for red cedar. Ash had the greatest total density on the quadrats and was well represented in all size classes up to 5 in. d.b.h., the greatest diameter recorded. No other species attained this diameter size on quadrats. Seedlings, saplings, or young trees of 12 species were present—a greater number of species than was on the youngest field. Saplings and young trees were both frequent and abundant.

Space in the tree layer of the oldest field was only 8%. The species contributing the greatest cover was ash, 77% (Fig. 15). There were 15 species of trees on quadrats on this oldest field. This size class representation for ash was complete from seedings to trees greater than 10 in. d.b.h. Pin oak, the only other tree found in the largest size class, was missing in the smaller size classes. Some individuals of wild black cherry, red cedar, sassafras, and basswood were present in the 4.0 to 9.9 in. d.b.h. size class. No seedlings of red cedar were found. The density and frequency of tree species were high compared to that of the younger fields. Total density of ash amounted to 286 individuals of all size classes for an area of 800 sq m. More tree species were represented on this oldest field than on either of the others with ash the most important.

The dominance of ash in the revegetation of the fields at Raritan Landing led to a study of its rate of growth as indicated by growth ring counts, heights, and d.b.h. (Figure 16). Thirty straight-trunked trees

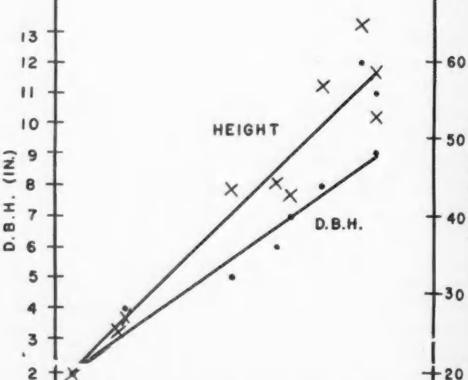

FIG. 16. The average number of growth rings and average height for each inch of diameter at breast height from 30 ash trees at Raritan Landing.

ranging from 2 to 12.6 in. d.b.h. were sampled at random from study areas. The heights and number of rings at breast height of these trees were averaged for each inch of diameter. Although this resulted in only a few points upon which to base a curve, it is sufficient to show the general rate of growth for ash on the Raritan Landing flood plain. The curves are missing for trees with fewer than 10 rings and

more than 31 rings at breast height, however, some trees are capable of attaining heights of almost 60 ft. and diameters of 9 in. or more by the time 30 rings at breast height have been formed. By adding about 5 yrs for a seedling to attain breast height the ages of those trees could be estimated as 35 yrs. It is possible, then, for ash trees on Raritan Landing to average approximately 2 ft of vertical growth and 0.3 in. diametral growth per year during their first 35 yrs.

Space in the shrub-sapling layer refers to the absence of both shrubs and saplings on the transect lines. However, cover values for shrubs and saplings have been computed separately. On the youngest field 55% of the total transect line was unoccupied by shrubs or saplings (Fig. 15). Of the total cover contributed by saplings only, American elm and wild black cherry contributed 35% and 34% cover respectively. The cover for red cedar was 10% and ash only one-half that value. Hawthorn and red cedar had equal values, 11%. Three shrubs, blackberry, silky dogwood, and poison ivy, had cover values greater than 20% each. A total of 9 trees occurring as saplings and 11 shrub species were encountered along the transect.

On the intermediate field, space in the shrub-sapling layer was 33%. The cover for ash was 42%, a value far in excess of that for the same species on the youngest field. American elm and wild black cherry contributed less than 10% cover each. The cover values for poison ivy and silky dogwood were 38% and 33% respectively. These values are greater than the values on the youngest field for the same species. Blackberry did not occur on the transect lines, although it was found elsewhere on the field. A total of 10 sapling species and 8 shrub species occurred along the transect.

The oldest field had only 13% space in the shrub-sapling layer. The relative importance with respect to cover for any single species is not as striking as it was on the younger fields. In other words there was less discrepancy between species in the contribution they made. Ash saplings had a cover value of only 7%. Basswood, not found on the younger fields, had 30% cover but was less frequent than American elm, ash, wild black cherry, red cedar, or hawthorn. The cover value for American elm was 18%, a greater value than it had on the intermediate field. Poison ivy was by far the most important species in this layer contributing 65% cover on the oldest field. Silky dogwood and Japanese honeysuckle had an actual cover of 12% and 17% respectively. A total of 18 species occurring as saplings and 9 shrub species contributed to cover. This large increase in number of sapling species as compared to the younger fields, associated with a reduction in single species dominance, is indicative of the trend of flood plain revegetation.

When the 3 fields on Raritan Landing are compared, there appears a striking succession of changes from one field to the next. Unfortunately there were no additional fields in comparable stages of succession to substantiate these vegetational changes. However, it may be presumed that these 3 fields show, in a general way at least, the trend of secondary succession on the natural levee of the flood plain. Comparison of this study with secondary successional studies on flood plains in other regions is not strictly possible as comparable data are lacking. In general, upland successional studies on abandoned fields have been more thoroughly done than flood plain studies. The heterogeneous nature of flood plain soils, moisture conditions, and the availability of suitable areas for study may well account for the lack of more complete information on bottomland succession. Oosting (1942) has dealt with the problem in North Carolina, and other workers have added their knowledge in other parts of the country (Featherly 1941, Turner 1931, Barclay 1924, Hotchkiss and Steward 1947).

The rate of secondary succession on the flood plain of the Raritan River is comparatively rapid. The rate of reinvasion is dependent upon many factors, among which the most important are the proximity of suitable species as a source of seed and a favorable environment for ecesis. Once plants are established the soil nutrients, the moisture relations, and the eventual effects of competition between species will greatly influence the progress of succession. The strip of woody species along the bank of the river, the hedgerows of trees and small but well developed "pin oak groves" in the vicinity of the Raritan Landing fields contain a large variety of species. The fields, wooded areas, and marshlands are frequented by a large number of birds throughout the year. The birds along with rodents and other animals common to flood plain areas greatly aid in the dissemination of seeds of certain species and wind, of course, is an effective agent of dispersion for the rest. Furthermore great numbers of seeds must certainly be deposited with the alluvium at times of floods. The soil of the Raritan River flood plain is quite fertile (Patrick *et al.* 1923), as such flood plains generally are. This soil, especially on the natural levee where the fields are located, is rather well drained (Fig. 4). The water table is usually less than 6 ft below the surface and hence water supply is never critical even during long periods of drought, at least for deep-rooted species. Thus it is reasonable to assume that succession would be rapid on such fields where seed source, facility of dissemination, and favorable growing conditions prevail. The rapidity of the succession, especially in the early stages on the fields at Raritan Landing, is reflected in the invasion by trees. Less conspicuously there are some indications that the herbaceous stages are of shorter duration than comparable stages on adjacent upland fields.

The flood plain fields were pastured for considerable time previous to the cessation of agricultural uses. The early herbaceous stages can be expected to have been influenced by this usage. The abundance of common pasture grasses reflect this. The starting point of natural revegetation thus began on fields

which had some plant cover, mainly grasses. The trend in the herbaceous layer as indicated by the fields studied shows a decrease in herb cover with an increase in time. This change is associated with a change in species composition and dominance.

A rather large cover value for goldenrods on the youngest field corresponds to a similar early upland stage in New Jersey as described by Bard (1952). However, on the uplands Andropogon follows the goldenrods, displacing them and often dominating large parts of fields for periods as long as 40 yrs after abandonment (Bard 1952). No such Andropogon stage occurs at Raritan Landing. Andropogon actually contributed very little to cover on any field. Instead, *Agrostis tenuis,* a pasture grass probably persisting from the time when the flood plain was used for pasture, was the most important species on the 2 youngest fields, but it did not appear to displace the goldenrods. Rather, they became established in the grass, possibly even during the time pasturing was going on. If anything, certain of them, at least *Solidago juncea* and *S. nemoralis,* increased in spite of the grass. It is probably the shading by trees and shrubs that caused a decrease in both the goldenrods and the grass.

Some 36 yrs after trees (greater than 1 in. d.b.h.) appeared, as indicated by the oldest field, an almost entirely new combination of herbaceous species occurs under the closing canopy of trees and shrubs (Table 3). These herbs are generally shade tolerant. The presence of a large ground cover of poison ivy and Japanese honeysuckle in the oldest field also greatly restricts summer herbs. Nevertheless, a rather large variety of species were present although their actual cover was small.

One of the most noticeable aspects of early stages of succession in this area is the presence of shrubs and vines, sometimes as scattered individuals, sometimes in clones *(Cornus racemosa, Myrica pensylvanica).* Shrubs and vines were rather well represented on the youngest field at Raritan Landing. Poison ivy had the greatest cover. Although shrubs, in general show an increase in cover values as the series of fields is studied in sequence, the progressive increase in dominance of poison ivy is most pronounced. This was also recorded by Bard (1952) in her upland study, in which she found this species was most important in the 60-year-old fields. A less obvious but interesting comparison may be noted with respect to silky dogwood. Nowhere did this species account for more than 1% cover in the upland succession (Bard 1952), while on the intermediate flood plain field, it was almost equal in cover value to poison ivy. Silky dogwood is characteristically a species of lowlands or moist sites, while poison ivy is ubiquitous in central New Jersey.

The first trees to invade the fields were red cedar, wild black cherry, and ash. The first of these was especially obvious on the youngest field. Saplings of American elm were frequent and contributed much to cover in the same field. This indicates that elm increases a little later in the succession than cherry, red cedar, or ash. With time ash cover increases tremendously; after 21 yrs ash completely surpasses all other species with respect to cover and density. This trend continues so that by the end of 36 yrs the fields may be dominated by a young ash forest. The rapid development of an ash forest within 36 yrs is strikingly different from the usual development of surrounding upland fields as described by Bard (1952).

As the ash forest develops, the species that preceded it are generally eliminated and a variety of new species appear in its understory. Wild black cherry and red cedar are overtopped by ash; they are suppressed, are in poor condition, and are not reproducing. Elm, on the other hand, is well represented by saplings. Basswood, pin oak, hackberry, and boxelder along with several other species are also present as saplings, and their presence suggests the future mixed composition of the forest. The percent of cover due to ash in the sapling layer of the oldest field is less than that for the younger fields. Thus ash, although reproducing some, will become less important in proportion as the other tree species increase.

Ash has been shown by others to be an important tree on flood plains and bottomlands. Oosting (1942) found it the second most frequent transgressive tree in a 36-year-old stage of a birch succession. In the same study, succession through sycamore revealed that ash had the highest reproduction, with elm second in a 35-year-old stand. Although bottomland succession varied in its early stages depending on a variety of circumstances, Oosting states, "All evidence indicates eventual maple-elm-ash dominance" prior to ultimate development.

On western flood plains the excessive silting of the Deep Fork River in Oklahoma killed off an oak-hickory flood plain forest and within 10 to 12 years a young forest of ash, cottonwood, and willow occupied the space between dead trees of the old forest (Featherly 1941). In the same state Penfound (1948) describes a green ash-American elm dominated area of the South Canadian River. Barclay (1924) working on primary succession, as indicated by denuded plots on the Mississippi flood plain in Minnesota, considered American elm and green ash as a subclimax stage of the mature flood plain forest.

The rapidity with which woody species invade flood plain areas has been noted by Turner (1931) in succession on artificial levees of the Illinois River Valley. American elm and silver maple attain sufficient dominance in 40 yrs so that he tentatively predicted an elm-maple climax attainable in 50 yrs. Ash was present along with pin oak, hackberry, and other species.

Secondary succession at Raritan Landing is thus somewhat similar to succession of other flood plains. In the first place, the development is comparatively rapid. Secondly, ash if not the most important species, generally plays a conspicuous role. The first

forests are generally composed of one or a few species, while later stages become quite mixed in composition with a change in dominance.

REED CANARY GRASS AREA

In places along the river's edge, especially below the confluence of the North and South Branches, occur low, flat areas dominated by *Phalaris arundinacea* (reed canary grass). These low-level flood areas vary from a few meters to 20 m in width. They are bordered by the river on one side and by the levee bank on the other. The areas are only about 1 m above the normal river level and are thus subjected to more frequent and forceful flooding than the levee proper. This flooding results in an accumulation of sand in the sod of grass. Where water movement is especially rapid, sloughs may be cut in the grass area. A slough of this kind is usually present at the base of the levee bank where shading by overhanging trees has reduced the vitality of the grass. Series of these sloughs give an undulating topography to the surface of the low level flood plain. Such an area near Landing Lane was studied in detail (Fig 14).

The transect which was extended for 200 m along this section of the flood plain was intersected by only 3 species of trees which together covered about one-third of the area. Boxelder contributed 23% cover, black willow 6%, and silver maple only 2%. Stems of silver maple were in reality upright branches of fallen trees whose roots remain embedded in the levee bank. These fallen trunks were completely hidden by the reed canary grass so that the upright stems looked and functioned like trees. Elsewhere on high hummock-like areas occasional sycamore, river birch, and ash trees were present. They were not abundant on the area studied in detail. In general, trees on the area bore indications of flood or storm damage with many sprouts arising from a single base.

Only one shrub was encountered, elderberry, and this contributed less than 1% cover along the 200 m. In the herb layer reed canary grass showed practically complete dominance. There was no unoccupied space in this layer and *Impatiens capensis* was the only other species to contribute more than 1% cover. Twelve other species listed in the section on flora (Fig. 7), each contributing much less than 1%, made up the total list of species on the transect.

Along the water's edge where water movement had been decreased by obstructions, a zone of emergent plants occurred. These were usually masses of Polygonum, *Pontederia cordata*, or *Zizania aquatica*.

Reed canary grass covers almost the entire low-level flood plain area (Fig. 17). Nichols (1916) also found this grass common in marshy areas along the Connecticut River. It grows to a height of 6 ft or more and flowers in June. By August the grass has produced a profusion of seeds, and many of the tall culms have fallen or been knocked down by storms and floods so that the grass is then only about knee deep. During the late summer months new shoots are produced at the nodes which break through the sheaths of the old leaves. These shoots root and

FIG. 17. Photograph of a reed canary grass area bordering the levee bank at Raritan Landing showing the winter aspect of the dominance of the grass. Trees are mostly sycamore, silver maple, river birch, and boxelder.

a new entangled mass of plants becomes established. The result is a dense, soft, springy, mattress-like mass of old stems with a green, meadow-like, new growth. This manner of growth virtually excludes all other species except in and around sloughs. The plants occupying these wet, grass-free sloughs are: *Pilea pumila, Boehmeria cylindrica, Polygonum coccineum, Solanum dulcamara, Geum canadense, Alliaria officinalis, Peltandra virginica, Acalypha virginica, Lysimachia nummularia*, and *Saururus cernuus*.

RIVER BANK

Near the river at Raritan Landing the trees of the levee had not been removed, at least for a long time. A wooded strip which varies in width but is usually not more than 30 m wide, borders much of the river. At places the strip is on the immediate bank of the river, or a low-level reed canary grass area may lie between it and the river. In any case there is a steep rise of at least 1 or 2 m forming a distinct bank. Two sections were studied in detail (Fig. 14).

As might be expected this river border strip of woodland was quite diversified. The two sections studied in detail bear this out (Fig. 18). On both areas there was a total of 19 tree species, which were those commonly found on other places along the river. One section of bank studied was dominated by silver maple, whereas the other section was dominated by ash and sycamore. Poison ivy, Japanese honeysuckles, bladdernut, and occasionally grape contributed heavily to cover and greatly increased the competition for light. The most important herbs were *Phalaris arundinacea, Alliaria officinalis, Hystrix patula, Impatiens capensis*, and *Tovara virginiana*. Others are listed in Figure 7.

The trees contributing the largest total basal area along the bank (Sect. 1, Fig. 18) in order of decreasing importance were: silver maple, sycamore, river birch, basswood, American elm, and white ash. At the other place studied they were: ash, hackberry, basswood, honey locust *(Gleditsia triacanthos)*, American elm, and swamp white oak *(Quercus bicolor)*.

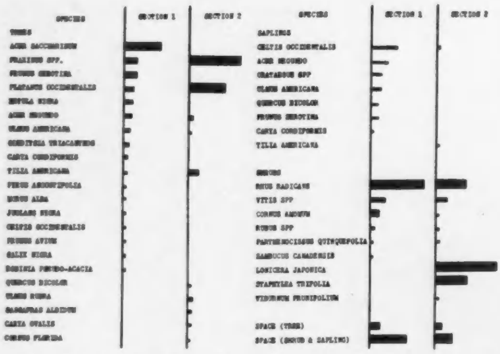

FIG. 18. Percent cover and frequency of trees, saplings, and shrubs occupying two sections of the bank of the levee at Raritan Landing. Section one lies opposite the youngest and intermediate aged fields (Fig. 14); section two lies opposite the oldest field. Data based on 15 transect segments of 20 m each at section one and 5 transects of 20 m at section two. Length of bar indicates % cover, width % frequency. Values for less than 3% cover and 20% frequency are indicated by a bar the size of that for *Pyrus angustifolia* at section one.

Silver maple and bitternut hickory were the only species found as seedlings. Saplings and sprout growth were abundant. Almost all the silver maples were multitrunked and had numerous sprouts.

The river bank vegetation at Raritan Landing is composed of species which are found generally throughout the flood plain of the river. Black willow, river birch, silver maple, sycamore, and boxelder are the species most characteristic of the river bank. These sprout readily and survive flood damage. They are probably favored by the relative high light intensities characteristic of the river bank habitat.

MARSH

At places along the river there are poorly drained areas which vary in size behind the natural levee. At Raritan Landing a rather extensive marsh has developed on such an area (Fig. 14). The plants occupying these areas are those characteristic of marshes in general and present striking seasonal aspects.

Many species of marsh plants grow in large masses and show some degree of zonation. *Leersia oryzoides* occasionally forms a rather definite border between the better drained soil of fields adjacent to the waterlogged soils of the marsh. Through the main portion of the marsh *Sparganium americanum, Typha latifolia, Carex stricta,* and *Acorus calamus* also form distinct bands. Although grasses and sedges prevail throughout the area, masses of Polygonum occupy wet situations, and *Lemna minor* seasonally covers the surface of the standing water.

The dominant shrub is silky dogwood, although crab apple and marshmallow *(Hibiscus palustris)* are conspicuous when in flower. Poison ivy and blackberry are abundant locally throughout the marsh. Trees are usually small and occur as scattered individuals of ash, elm, pin oak, swamp white oak, and honey locust. Where wooded areas are adjacent to the marsh, there is a migration of trees onto the fringes of the march (Fig. 19).

FIG. 19. Transition from pin oak woods to marsh showing young trees and shrubs invading the marsh at Raritan Landing.

In winter the color aspect of the marsh is a dull gray-brown except for the red stems of the silky dogwood. With the coming of spring and early summer the rich herbaceous growth gives a lush green color to the marsh. During the summer and the onset of fall Solidago, *Bidens coronata, Eupatorium purpureum, Vernonia noveboracensis, Aster novae-angliae,* and other plants (Fig. 7) give a very colorful aspect to the marsh.

GENERAL ASPECTS OF THE RARITAN RIVER BASIN

The extent of the Raritan River flood plain between Burnt Mills and New Brunswick has been mapped from air photos (Fig. 3). Evidently only a small portion of the flood plain is heavily covered by trees; many areas are pastures or newly brush-covered. Several industrial sites are found along the river, indicating the economy of much of the lower Raritan River Valley. The valley has grown enormously in population, the number of people employed in industry having increased from 6,700 in 1901 to over 40,000 in 1952 (Hurd 1954). Thus the emphasis on land use has been shifting away from agriculture especially in the lower part of the valley. There land formerly used agriculturally has either been put to non-agricultural use or allowed to remain idle. Some of the idle fields have become revegetated, but only in remote parts of the valley is it possible to find stands of large trees.

The numerous habitats present on the Raritan River flood plain support a large number of plant species and if allowed to revert to its natural condition the flood plain will support luxuriant vegetation diverse in composition. There would be the same general character to the vegetation throughout the entire system, although the composition of the predominantly eroding upper part of the river would

differ in detail from the predominantly depositing areas of the downstream end of the river. In general, recognizing the differences in vegetation along the length of the river, there are four physiographic features with major plant communities on the Raritan River flood plain. (1) The newly depositing sand bars and river banks have an extensive herb cover and established bars have profuse growth mainly of willow, river birch, and sycamore. These bars may develop into islands rich in vegetation. (2) The natural levees or outer flood plains support magnificent forests consisting of a mixture of largely mesophytic species. Once established these forests may ultimately be destroyed by the slow process of stream meandering. (3) The inner flood plain also supports a large mixture of plants, but these areas are wet and support primarily boxelder, pin oak, red maple, river birch, swamp white oak, and black gum. Marshes may exist in places on these areas, but with continued accumulation of alluvium the trees will become established. (4) The terrace which in places borders the flood plain has the potentiality of a mesic forest that could be expected to have a high percent of such species as sugar maple, basswood, beech, and some flowering dogwood.

The present vegetation of the flood plain of the Raritan River is only suggestive of the potential development of its flood plain forests. If revegetation of former agricultural land continues to be permitted, a splendid mixed forest will ultimately grow there with the forest floor covered with showy flowering herbs changing with the seasons. The diversity of habitats within small areas makes a flood plain ideally suited for natural area reservations in such highly populated areas as the lower Raritan Valley. The increasing recognition of the value of natural areas as part of park systems makes it possible that certain parts of the flood plain system may ultimately be allowed to grow back to their original magnificence.

SUMMARY

1. The flood plain of the Raritan River is derived from diverse geologic materials, since the river flows over three of New Jersey's four geologic provinces.

2. Flood waters deposit the finer particles of alluvium at a greater distance from the river than the coarser particles. This results in the development of a flood plain which has a greater percentage of sand on the river bank than it has farther from the river. The dynamics of such deposits were apparent in a soil profile on the natural levee or outer flood plain at Raritan Landing.

3. Floods on the Raritan River are unpredictable and range from none to about 16 days of flooding a year. The more recent trend as interpreted from existing records seems to be toward higher annual average temperatures, lower precipitation, and fewer floods. Monthly records show that March has the most floods, although the greatest average monthly precipitation is in summer when temperatures are high, plant cover dense, and floods scarce.

4. The flood plain forest at Burnt Mills is composed of a large number of species. Within this forest several plant communities are evident: the outer flood plain with mesophytic species, the diverse inner flood plain forest, and the sugar maple dominated terrace. River banks and islands show successional trends on newly deposited alluvium which reflect the dynamics of stream action.

5. The mesophytic forest of the outer flood plain at Burnt Mills and the vegetation of Mertensia Woods are on similar sites and are comparable in many respects.

6. Secondary succession at Raritan Landing is rapid and the rapidly growing ash trees play an important role in early forest formation. Pasture grasses rather than Andropogon are important in early stages of the revegetation of formerly pastured fields.

7. The tree species occupying banks of the levee are characteristically willow, river birch, sycamore, and boxelder, although species of the mature forest of the levee are present. The river bank may be bordered by a reed canary grass fringe. Behind the levee marshland may exist.

8. The present vegetation of the Raritan River flood plain shows that the utilization of the flood plain for agricultural purposes is decreasing. Thus more land is reverting to its natural condition, or is being occupied by industrial sites or recreational areas.

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COMPARATIVE REPRODUCTIVE BEHAVIOR AND ECOLOGY OF FOURTEEN SPECIES OF DARTERS (PISCES-PERCIDAE)

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INTRODUCTION

Comparative behavior has evoked considerable interest in recent years. The study of comparative behavior contributes an additional insight into the evolution of animals which has been primarily based on morphological grounds. "Biological characters are of paramount importance to the classifier, for habits and behavior are certainly deeply rooted and are often the product of a very ancient evolution." (Delacour & Mayr 1945). A comparative study of behavior also gives us a better understanding of basic behavioral and ecological problems, many of which are still poorly understood.

A fairly voluminous literature exists on the behavior and life history of many different species of fishes. For the most part this material has not been integrated and few comparative studies are available. Baerends & Baerends-van Roon (1950) published a general survey of the nest-building and oral-incubating cichlid fishes. Breder (1936) compared the reproductive habits of the nest-building North American sunfishes. The present study of the darters is also of a broad survey type. There are few detailed comparative studies of related species of fish. Outstanding is that of the mating behavior of the two sympatric xyphophorin fishes by Clark, Aronson & Gordon (1954). Of a somewhat different nature are Raney's (1947) field observations on the complex relationships between stream fishes, such as the utilization of *Nocomis* nests for egg deposition by other fishes. The evolution of behavior has recently been considered for certain groups, notably mammals (Beach 1947; Tinbergen 1951, 1953) and birds (Kendeigh 1952; Lorenz 1951, 1952, 1953). Sixteen studies have been published that deal specifically with some aspect of ecology or behavior of the darters. These are mostly limited to incomplete descriptions of breeding habits and to age and growth problems. Raney & Lachner (1939), Fahy (1954) and Winn (1958) reviewed the literature on the breeding habits of these fishes. The individual accounts of the observations on each species and comparisons with previous studies have been given by Winn (1958).

The information presented in this paper is an attempt to treat comparatively the reproductive behavior and ecology of 14 species of darters which exhibit a great variety of habits and form, within one subfamily, Etheostomatinae. Each aspect of the habitat, sexual dimorphism, migration, reproductive season, territory, courtship, spawning act, care of eggs, sex recognition, and eggs is described for most of the species and is discussed from a comparative viewpoint. A phylogeny of behavior is presented which is compared with the phylogeny based entirely on morphology. The decisions on phylogeny based on behavior and on morphology are shown to be in general agreement.

The darters are an interesting and valuable group for the study of behavior. They utilize a large number of different microhabitats found in running waters and in the littoral zones of lakes. Their reproductive behavior varies from the free scattering of eggs over gravel to the laying of eggs in a compact unit on the underside of a rock. Some species deposit their eggs on organic debris, algae and on higher aquatic plants. The primitive forms exhibit little sexual dimorphism whereas the more specialized types are extremely dimorphic in coloration. The colors of the males in many species include bright blues, greens and reds. Migrations, territories, spawning acts, care of eggs, and other aspects of behavior manifest both interspecific and intraspecific variation. Darters can be readily studied in the field as well as in the laboratory. Thus the supplementary results

of these two approaches can be reconciled and as an outgrowth, a clear, concise, and more natural representation of the group's behavior is achieved.

The darters form an important segment of the freshwater fish fauna of North America. Except for the invasion of one stream tributary to the Pacific Ocean in Mexico, the darters are confined to the Atlantic drainage. The name darter is derived from the habit these fishes exhibit in swimming in short dashes along the bottom. The family Percidae first appears in the Eocene (Berg 1940), but it seems likely that the subfamily Etheostomatinae is of much more recent origin. The darters appear to be the result of a recent "explosive" and adaptive evolution. There are about 100 species in eastern North America today.

All the species of darters found in the Ann Arbor, Michigan area were chosen for study as well as a few representatives of other darters from Kentucky and Tennessee. Field observations were made on 13 species in Kentucky, Michigan and Tennessee. The fourteenth species was studied only by Raney & Lachner (1939).

The species treated in this paper, arranged in order of complexity of behavior as nearly as possible, are as follows: *Percina caprodes* (Rafinesque); *Hadropterus maculatus* (Girard); *Etheostoma (Poecilichthys) caeruleum* Storer; *Etheostoma (Poecilichthys) spectabile* (Agassiz); *Etheostoma (Doration) saxatile* (Hay), which has been recently referred to as *Etheostoma stigmaeum* (Jordan) (Bailey, Winn & Smith 1954); *Etheostoma (Poecilichthys) exile* (Girard); *Etheostoma blennioides* Rafinesque; *Etheostoma (Microperca) microperca* Jordan and Gilbert; *Hadropterus (Cottogaster) copelandi* (Jordan); *Etheostoma (Ulocentra)* sp., Barren River, Kentucky and Tennessee; *Etheostoma (Ulocentra)* sp., Green River, Kentucky; *Etheostoma (Boleosoma) nigrum* Rafinesque; *Etheostoma (Poecilichthys) maculatum* Kirtland; and *Etheostoma (Catonotus) flabellare* Rafinesque. The generic nomenclature is that used by Bailey (1951). The most often used generic name in the recent past is given in parentheses.

I am greatly indebted to Dr. Robert R. Miller for his enthusiastic interest and generous support towards the completion of this work. Among those who have aided in collecting, I wish to acknowledge the help of Jorge Carranza, Quentin Pickering and James Keleher. I wish to thank Carolyn P. Winn who has aided in the preparation of the manuscript and with the seining. The help of Elsa Hertz, who typed many of the preliminary drafts, is greatly appreciated. William Brudon inked and improved pencil sketches of figures 1, 2, 3, 6, and 7 and drew figures 4 and 5. Drs. Reeve M. Bailey, William Fahy, Clark Hubbs, Edward C. Raney and John Williams have kindly supplied data used in this comparative study. The critical reading of the manuscript and the many helpful suggestions by Drs. Lester R. Aronson, Marston Bates and C. M. Breder, Jr. are sincerely appreciated. A grant from the Revolving Research Fund of the American Society of Ichthyologists and Herpetologists to aid this program is gratefully acknowledged. This paper is a contribution of the Museum of Zoology and Zoology Department, University of Michigan, and the Zoology Department, University of Maryland.

PLACES AND METHODS OF STUDY

Much of this work was carried out in or near Ann Arbor, Michigan, but some of the observations were made in Kentucky and Tennessee. A list of the localities where the major portion of the observations were made or where laboratory fish were collected has been given by Winn (1958). All except Douglas Lake in northern Michigan and three localities in Kentucky and Tennessee were in the immediate vicinity of Ann Arbor, Michigan. Many other localities were visited and collections were made over a period of three years throughout all seasons.

The various behavioral components were on some occasions recorded by means of a tally system. In this way the frequency of occurrence, under the described conditions, was obtained. Usually the fish were studied until a particular action was observed 20 times or more. Frequently a trait was observed over 100 times. Under the conditions of study, variation of behavior was difficult to describe, but a conscious effort has been made to emphasize the variation rather than to limit the description to some mode or average which would make the behavior seem more rigid than it is. Some difficulties were encountered with visual observation and further work will profit from the use of a camera or some behavior recorder such as the one discussed by Clark, Aronson & Gordon (1954).

Two limiting aspects of the problem should be mentioned here. First, only a few selected populations of each species have been studied. There is ample evidence of geographic variation of behavior which is not considered at this time. Secondly, only a few species from each subgenus were observed.

In a few cases experimental procedures were used. Many factors were found to be important in the aquarium work. It was found that the fish acted similarly under rather wide variations of light and condition of water. Differences of behavior between species were noted under strong illumination (No. 2 photoflood). The expression of territorial behavior and sex recognition were often affected by the space factor. There was a certain minimum space in which a normal territory was established. In a few species, reproduction ceased if the water depth was two or three times less than the natural depth in which they spawned. The exact limits of the various factors were not defined precisely but it was usually ascertained that they did not vary more than under normal field conditions. Once the normal conditions were established, a great deal of useful information was obtained by placing the fish in aquaria under these abnormal or, in nature, infrequent situations.

Although most darters live in turbulent currents,

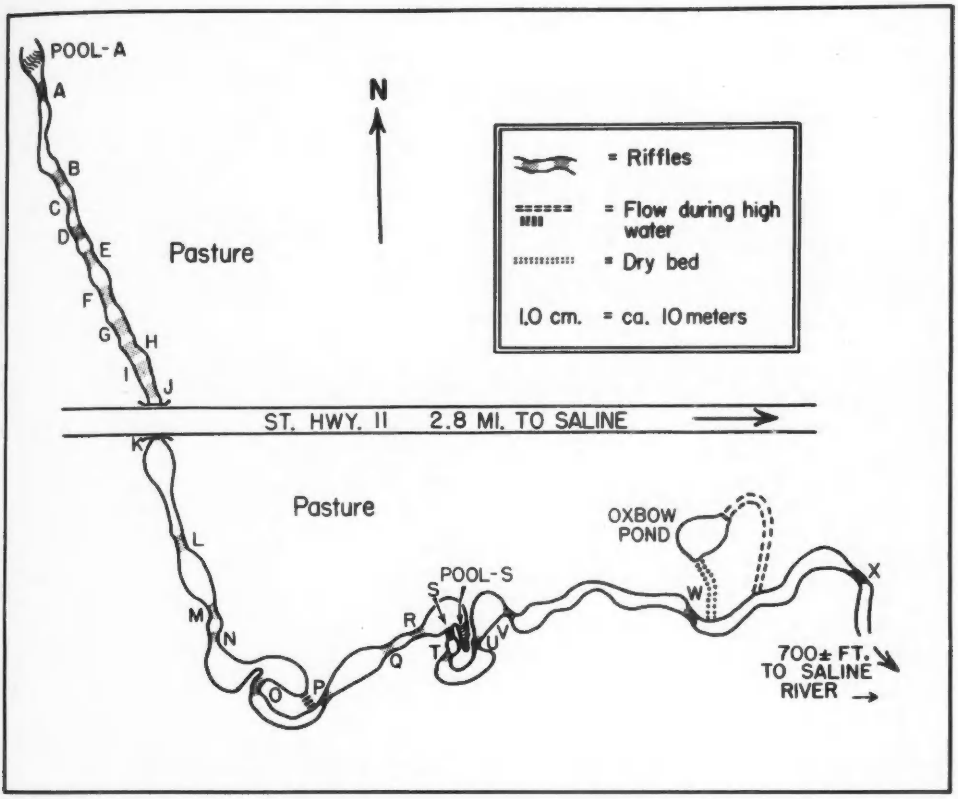

FIG. 1. The small section of stream where some of the riffles and two of the pools were sampled continuously for one year and a half. See text for explanation. The bold dashed line near riffle P represents the stream course in 1951, which subsequently shifted so that water now flows across this section only during floods.

they laid at least one normal batch of eggs in aquaria where the only water movement was from an air bubbler or sometimes from a very slow flow of water. The structural forms of the population that could not be exactly duplicated in tanks were a deep-water area for the female to escape to and the uni-directional orientation of the population caused by the current.

In order to study the seasonal habitats and movements, a series of riffles in a tributary to the Saline River was systematically seined throughout 14 months (Fig. 1). Seine hauls were taken with a 10 x 4 feet x 0.25 inch mesh common sense minnow seine. The net was set at the base of the plot and the area was kicked from three meters above downstream to the net, which was then lifted. After counting the individuals caught the fish were returned to the stream. The full length of the net was used except at stations A, O, S, W and X, where the full width (1-2 meters) was seined. Young individuals were not counted until January when they were ordinarily large enough to be held by the mesh. Seine hauls were taken every 3 or 4 weeks for 15 months.

Detailed substrate measurements were taken in order to determine whether or not certain darters were restricted by the type of bottom. The data are given in Table 1, which does not include any species represented by a total of less than 5 individuals throughout the 14 months. Numbers and letters were given to all the riffles (Fig. 1). A block sample of stations (A, B, N, O, S, W and X) was chosen because they had fine gravel bottoms or were exceptional in some respect. Only one fine gravel riffle, T, comparable to S, was not utilized. Of the remaining 16 rubble riffles a block of 6 (E, H, J, L, P and R, Fig. 1) were chosen by use of a table of random numbers. In order to add two different habitats to our samples, pool A, continuous with the stream, and S, a shallow side pool, were included.

It was evident from measurements of the gravel that three types could be distinguished by size alone. Later evidence exhibits a correlation between the distribution of the darters and these three types. The substrate was measured with a set of U. S. Standard Sieve Series with the following mm openings: 101.6, 76.2, 50.8, 26.67, 18.85, 13.33, 6.68, and

TABLE 1. Species and numbers of individuals of the genus *Etheostoma* collected from stations in the tributary to Saline River during 1952 and 1953.
(blen=*E. blennioides*, caer=*E. caeruleum*, flab=*E. flabelare*, micr=*E. microperca*, nigr=*E. nigrum*, spect=*E. spectabile*; M=moderate water level, L=lower, H=higher; wherever 2 seine hauls were taken the numbers represent the average to the highest whole number)

		Spawning							Spawning			Substrate	Surface velocity ft. per sec.	
	Date	V-11	V-30	VI-23	VII-13	XII-15	III-8	III-29	V-3	V-24	VI-6	VI 1953	V-31 1953	IV-14 1954
	Temp. °C	15°	17°	23°	26-30°	1-2°	0.5°	5.5°	16°	18°	24°			
	Water Level	M	M	L	L	M	H	H	M	M	L			
	Seine Hauls	2	2	1	1	1	2	2	2	2	2			
STATION	SPECIES													
Riffles A	flab	2	1	0	0	2	0	3	2	2	0	Fine Gravel	0.88	1.22
	caer	1	2	5	0	0	2	0	3	2	0			
	spect	1	1	1	0	0	0	2	17	3	0			
B	blen	0	1	0	0	1	0	2	1	3	0	Coarse Gravel	0.22	1.04
	micr	0	0	0	0	0	0	3	1	1	0			
	flab	1	1	0	0	0	1	0	2	0	0			
	caer	4	2	0	0	3	2	10	5	2	2			
	spect	5	7	0	1	0	1	1	0	3	0			
E	blen	1	3	0	0	0	2	0	12	2	0	Rubble	0.95	2.14
	flab	1	1	0	0	1	4	1	1	2	1			
	caer	4	3	3	3	2	2	5	2	5	2			
	spect	1	0	0	0	0	0	2	1	0	1			
H	blen	2	3	0	0	0	0	1	2	0	0	Rubble	0.88	1.39
	flab	2	1	0	0	0	4	1	2	5	1			
	caer	15	7	2	0	0	3	8	5	9	3			
	spect	1	0	0	0	0	0	0	0	0	3			
J	blen	1	2	0	0	0	0	1	1	0	0	Rubble	1.24	2.78
	flab	1	2	0	0	0	3	3	4	4	1			
	caer	6	3	0	0	1	0	1	7	18	1			
L	blen	4	1	0	0	0	1	2	3	1	0	Rubble	0.99	1.87
	flab	2	1	1	0	0	1	2	1	3	2			
	caer	16	8	4	0	3	1	0	5	15	4			
N	blen	1	0	0	0	0	2	1	0	0	0	Coarse Gravel	1.13	1.22
	flab	1	0	0	0	0	2	0	2	2	0			
	caer	42	16	2	0	1	7	4	20	25	0			
	spect	1	1	0	0	0	2	0	2	1	0			
O	blen	2	0	0	0	0	1	1	0	0	0	Fine Gravel	1.02	2.78
	caer	20	11	0	0	0	0	0	8	12	1			
	spect	9	4	0	0	0	1	1	26	9	1			
P	blen	1	1	0	0	0		3	0	0	0	Rubble	1.41	2.68
	flab	0	1	1	0	0		2	1	1	0			
	caer	9	4	1	0	1		0	4	8	0			
R	blen	2	0	0	0	0		2	1	0	0	Coarse Gravel	1.60	2.32
	flab	3	1	1	0	1		3	2	2	0			
	caer	26	18	3	0	0		5	25	14	1			
	spect	1	1	0	0	0		0	2	0	0			
S	blen	0	0	0	0	2	1	2	0	0	0	Fine Gravel	0.84	1.96
	caer	14	4	0	0	1	0	1	21	8	0			
	spect	16	8	0	0	0	0	1	36	6	0			
W	blen	0	0	0	0	1	2	1	1	0	0	Coarse Gravel	1.02	2.23
	nigr	1	2	0	0	0	4	2	2	0	0			
	caer	27	26	2	0	0	0	0	8	5	0			
	spect	6	3	0	0	0	2	1	19	0	0			
X	blen	0	1	0	0	3	2	1	1	0	0	Coarse Gravel	1.02	2.14
	flab	1	0	1	0	0	0	2	6	0	0			
	nigr	0	0	0	0	0	1	3	2	0	0			
	caer	12	14	0	0	0	0	0	21	7	0			
	spect	3	2	0	0	0	0	6	18	2	0			
Pools A	micr			3	0	8	0	7	10	6	2	Silt		
	nigr			0	0	3	0	0	3	0	0			
	caer			4	4	0	0	0	1	0	0			
	spect			12	3	6	0	0	2	0	0			
S	micr			2	0	0		0	4	4	2	Silt		
	nigr			0	1	1		0	4	1	0			
	caer			0	0	2		2	0	0	4			
	spect			1	0	3		7	1	2	4			

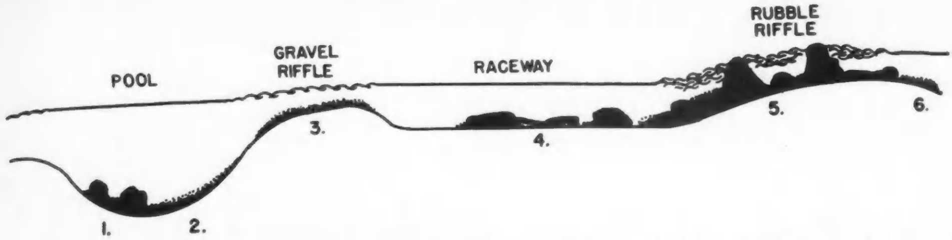

FIG. 2. Section of gravel-rubble stream showing various reproductive habitats occupied by darters. *P. caprodes* utilizes 4, with a fast current, and 5; *H. maculatus* 2 and 4, when covered with fine gravel; *E. caeruleum* 3, 5 and 6; *E. spectabile* 3 and 6; *E. saxatile* 3 and 6; *E. blennioides* 5; *E. (Ulocentra)* spp. 1 and 4; *E. nigrum* 4, with a slow current; *E. flabellare* 4, but with a faster current; *E. maculatum* at the head of 5.

3.38. The volume of each size group of stones was determined for the two square-foot samples collected from each plot. At the 5 stations, E, H, J, L and P, the substrate was designated rubble because the greatest volume of rock was well over 50.8 mm in least diameter. Only R of the original block sample fits another category. Stations B, N, R, W and X were designated coarse gravel because the greatest volume of rock was between 18.85 and 50.8 mm in least diameter. At stations A, O and S, the greatest volume of substrate material was below 13.33 mm in diameter (fine gravel). One other characteristic of the latter three stations is that the greatest single volume was in the smallest size group, less than 3.38 mm in diameter.

Current measurements were taken with a Gurley current meter, the accuracy of which was hampered by the shallow depths on May 31, 1953 (Table 1). The depth and width of the stream varied considerably throughout the year. In general, all the riffles were shallow except for Station B which was a deeper raceway-like area, near the head of a series of riffles and below a pool-like area. Stations A, O, S, W and X were slightly narrower than the others. There is no evidence that the width or the depth of these stations, except possibly station B, had any direct effect on the reproductive behavior of the darters concerned.

HABITATS AND ASSOCIATES

The habitats of the various species of darters was analyzed in order to understand better their behavioral adaptations to the environment. Both interspecific and intraspecific habitat differences exist in the darters. The diversity among species is based on variations in the microhabitat which lessen or eliminate competition for space. Within a species there are seasonal, age and sexual differences in habitat selection. A large number of non-percid fish associates are commonly found with the darters during the breeding season. The spatial and temporal relations of these fish are so arranged that very little, if any, interspecific competition for reproductive sites takes place.

General: Some species have wide geographic ranges whereas others are more restricted. *Percina caprodes, E. exile, E. microperca, H. copelandi* and *E. nigrum* breed in comparable habitats of lakes and streams. *Etheostoma flabellare* and *E. blennioides,* although usually stream-breeding species, have been collected in Lake Erie (Turner 1921), and *E. flabellare* has been reported from a few lakes (Hubbs & Lagler 1947). It is not clear from the above papers whether these species spawn in lakes. *Hadropterus maculatus,* although mainly found in streams, probably does breed in lakes. *Etheostoma caeruleum, E. spectabile, E. saxatile, E. (Ulocentra)* spp. (Barren and Green River forms) and *E. maculatum* breed only in streams. A summary of the general reproductive habitat of the species examined in this study is given in Table 2.

It is convenient to divide the stream habitat into three ecological parts with appropriate subdivisions each occupied by different species of darters. The three sections are called the riffle, the raceway and the pool (Fig. 2). The raceway is intermediate between the riffle and the pool in depth of water, rate of flow, and substrate, and its depth is usually quite uniform. The riffle, raceway, and pool may each be divided into two subtypes, either with a fine gravel bottom or with a rubble (large rocks and some gravel) bottom. The pool and raceway have another type—a silt-covered bottom which is not utilized as a breeding area by any of the darters, except where vegetation occurs. In limestone regions, the bottom may consist of smooth rock with occasional fractures. The heads and bases of riffles are also suitable habitats for the breeding of some species. Many intermediate situations involving the three types occur.

The shoal zone of lakes and comparable stream habitats are used as breeding places. The species found depends on the nature of the bottom, which may be sand, gravel, sand and rock, or detritus with thick vegetation. Such species as *P. caprodes, H. maculatus, H. copelandi, E. exile* and *E. nigrum* have fairly wide tolerances for changes in the rate of water flow. However, the substratum selected for egg deposition usually has narrowly prescribed limits.

Reproductive Seasons: The following descriptions are concerned with the reproductive microhabitat. *Etheostoma (Ulocentra)* spp. (Barren and Green River forms) and *H. maculatus* utilized pools and raceways. The former species laid eggs on large rocks

TABEL 2. Generalized Summary of Reproductive Data on Fourteen Species of Darters (*Percina, Hadropterus,* and *Etheostoma*)

Species	Reproductive Habitat	Reproductive Period	Size of Females[a]	Sexual Dimorphism and Sex Recognition	Territorial Defense	Size of Territory	Spawning Position	Egg Site	Average No. Eggs Laid[b]	Female Spawnings with One Male and Eggs Per Spawning
P. caprodes	Lake shores; stream riffles, and raceways	April-May	62-65	Slight; none to weak	None, to weakly intraspecific around female	None to moderate	Male on female's back; horizontal	Sand and gravel	±2000	1or 2; 10-20 or more eggs
H. maculatus	Stream pools and raceways, sand or gravel	April-May?	51-53	Slight to moderate; weak	Weakly intraspecific around female	Moderate	Male on female's back; horizontal	Sand and gravel	1758	?
E. caeruleum	Stream rubble or gravel riffles	April-May	40-44	Extreme; strong	Strongly intraspecific around female	Moderate	Male on female's back; horizontal	Gravel	880	1 to several; 3-7 eggs
E. spectabile	Small streams, fine gravel riffles	April-May	36-42	Extreme (color); strong	Strongly intraspecific, around female	Moderate	Male on female's back; horizontal	Gravel	1254	1 to several; 3-7 eggs
E. saxatile	Streams, gravel riffles	March-April? Ky. Tenn.	34-39	Extreme (color); strong	Strongly intraspecific around female	Moderate	Male on female's back; horizontal	Gravel		1 to several; 3-7 eggs
E. exile	Lake shores or slow streams with organic debris	April-May	41-43	Extreme (color); weak to strong	Strongly intraspecific, stationary by shore	Large	Male on female's back; pair at 0° to 45° angle	Organic debris and fibrous mud banks	1619	1 to several; 3-7 eggs
E. blennioides	Streams, rubble riffles with algae or moss	April-May	51-55	Extreme (color); strong	Strongly intraspecific, interspecific tendency, stationary by shore	Large	Male on female's back; pair from 0° to 90° angle	Algae and moss	784	Several; 4-7 eggs
E. microperca	Vegetated lake shores or stream pools	Last of April-June	27-30	Moderate (color) P_2 extreme; weak to strong	Weak to strongly intraspecific, stationary by plants	Moderate	Male on female's back; pair from 0° to obtuse angle	Aquatic plants	858	Many; single eggs
H. copelandi	Lake shores, stream gravel raceways	July	39-44	Moderate; strong	Strongly intraspecific, stationary by rock	Large	Male on female's back; horizontal	Gravel	721	One to several; 4-10 eggs
E. (Ulocentra) sp. Barren R.	Stream pools, raceways and shelves of limestone rock	Early April-mid-May	36-40	Extreme (color); strong	Strongly intraspecific, interspecific tendency, stationary by rock	Large	Male on female's back; pair from acute to obtuse angle	Large rocks, and breaks in limestone shelves	798	Many; single eggs
E. (Ulocentra) sp. Green R.	Stream pools, raceways and shelves of limestone rock	Early April-mid-May?	35?-40	Extreme (color); strong	Strongly intraspecific, interspecific tendency, stationary by rock	Large	Male on female's back; pair from acute to obtuse angle	Large rocks, and breaks in limestone shelves		Many; single eggs
E. nigrum	Lakes or slow streams with rubble	May	42-46	Extreme (color and fins); strong	Interspecific by rock nest	Small	Male beside female; upside down	Underside of rocks, etc.	1043	In clutches of 30-200 eggs laid singly
E. maculatum	Streams, rubble riffles or heads of riffles	Mid-May-Mid-June	40-47	Extreme (color and fins); strong?	Interspecific by rock nest?	Small?	? upside down	Underside of rocks	242	In clutches that average 65 eggs laid singly
E. flabellare	Stream rubble raceways or slow riffles	May	av. 42	Extreme (color and fins); strong	Interspecific by rock nest	Small	Male beside female; upside down	Underside of rocks	449	In clutches that average 34 eggs laid singly

[a]standard length in mm. of 2-year-old fish. [b]by 2-year-old fish.

and on the edges of broken surfaces of limestone bedrock whereas the latter laid eggs in coarse sand or fine gravel. *Percina caprodes* utilized sand or gravel-bottomed raceways, some riffles, and sand shoals of lakes. *Etheostoma caeruleum* spawned on riffles with rubble and gravel or just gravel (Table 1 for April and May). *Etheostoma spectabile* utilized only riffles with fine gravel and a slow current (Table 1). *Etheostoma caeruleum* and *E. spectabile* bred abundantly in streams at points where cows came for water. The cows apparently helped to keep the fine gravel riffles large and free of silt. *Etheostoma saxatile* spawned on fine gravel riffles and gravel-bottomed heads of rubble-covered riffles. *Etheostoma exile* bred in the slow current of streams that contained some vegetation and submerged fibrous root banks. This species also bred near the shores of lakes over areas of fibrous root and organic debris; in the two sites studied, a sand bottom was associated with these areas. *Etheostoma blennioides* spawned only on swift, rubble-covered riffles where the large rocks had heavy growths of *Cladophora* and/or *Fontinalis* (a green alga and moss). *Etheostoma microperca* bred in heavily vegetated pools, backwaters or lake shoals. *Hadropterus copelandi* bred in raceway-like gravel-covered areas of large streams or along lake shoals. *Etheostoma nigrum* bred in pools, slow raceways, and the shallow waters of lakes which had large rocks, logs or other suitable objects for egg deposition on the bottom. *Etheostoma maculatum* laid eggs under rocks found at the head of or in the deeper parts of riffles (Raney & Lachner 1939). *Etheostoma flabellare* spawned in rubble-covered raceways or slow, rubble-covered riffles.

Non-breeding Season: The habitats in the non-breeding season were sometimes strikingly different from those of the reproductive season. This is illustrated in Table 1, where the darters are shown to be present on riffles during April and May but absent at other times of the year. For most species the habitat change was accomplished within a few weeks after the reproductive season. This occurred between the May and June collections (Table 1). The adults of *E. caeruleum*, *E. flabellare*, and *E. blennioides* remained in fast, large, rocky riffles after the reproductive season; the first and last species found in some small rocky riffles with a fast current during the breeding season went onto fast, large, rubble riffles. Adults of *E. caeruleum* left the fine gravel riffles. Some individuals of *E. flabellare* left the sluggish riffles to remain in faster rock riffles during the winter months. The adults of *E. blennioides* generally remained on the same rapid-like areas farther downstream. In the outlet of Portage Lake, *P. caprodes* migrated to deeper water of either the lake or Huron River, although it is not known which course was taken. In Douglas Lake, *P. caprodes* was found in the deeper waters off shore in the non-breeding season. *Hadropterus maculatus* occurred in deep, often silt-covered pools. Adults of *E. spectabile* left the fine gravel riffles to remain in silt-covered vegetated margins of raceways with slow currents or in pools with slow currents. It was suspected that in midwinter individuals of *E. spectabile* buried themselves in the soft mud. Seine hauls over a small mud area yielded no darters until the mud was completely roiled up and then numerous adults were caught. However, when the temperature was 1.5°C, *E. spectabile* was observed swimming under the ice in a permanent pool in Rouse Drain. After breeding, *E. microperca* and *E. exile* went into the deep waters of lakes or into deep pools of streams. Both species were found in the winter in the thick organic debris and plant zone in 4 ft of water (Whitmore Lake). *Hadropterus copelandi* left the edges of streams and lake shores to go into deeper water immediately after spawning. *Etheostoma nigrum* moved into deeper water in the lakes or stayed in the silt pools and slow-flowing raceways with sand or silt bottoms. Heimburger (1913) described the summer habitat of this species in a lake as the shallow shore zone with silt. *Etheostoma maculatum* stayed in the deeper parts of riffles in the winter (Raney & Lachner 1939). The non-reproductive habitats of *E. saxatile* and the two forms of *E. (Ulocentra)* sp. were not studied, although the former species was not found on gravel riffles at the end of a spawning season.

Age and Sex Differences: Many of the young fish in their first fall and winter were usually found in different habitats from those occupied by the adults. This was particularly true in winter of the rock-riffle inhabitants, such as *E. blennioides, E. caeruleum* and *E. flabellare*. The young were found more often in the raceways and smaller pools. Furthermore, in the above three rock-riffle species, the larger adults were always found in the faster and deeper parts of the riffles which usually contained larger rocks. Fahy (1954) found such a size segregation for *E. blennioides*. Many of the young of *E. spectabile* were scattered over the sand or silt stream bottom near the areas where the adults and some yearlings were found. It is not known whether the other species show this type of distribution.

Habitat differences were observed between the sexes of many species. During the breeding season, females went up on the riffles or areas occupied by males only when ready to spawn. In the non-reproductive season some of the adult females were found in the areas where the young or yearlings occurred. Fahy (1954) showed this to be true for *E. blennioides* and my data indicate the same behavior. It also appeared to be true for *E. caeruleum*, *E. flabellare* and *E. spectabile*. Segregation by size or sex was inconspicuous for the lake or slow-current species, although it may occur.

Distribution in Plots: Up to this point we have given the general distributions based on season, age and sex. These were based on the sampling of many darter streams. In order to obtain detailed data on the distribution of different species of darters one series of riffles in the tributary to Saline River (Fig. 1) was seined systematically for one winter

and two springs (spring 1952 through spring 1953). The data illustrate in detail the reproductive microhabitat of 6 species which were common in the short section of the stream and also show the change of habitat that occurred before and after the breeding season (note the increased numbers in April and May, Table 1).

All the darters, except a few scattered individuals, left the riffles after the reproductive season, when the water flow was considerably decreased. Collections taken on August 3, August 24, September 13, October 11, 1952 and April 19, 1953, were similar to the hauls for July 13, 1952. Stream flow began to increase in November to March during which time a few scattered individuals reappeared on the deeper riffles. The darters slowly increased in numbers on the riffles until the breeding season, but there were significant increases in the population size during the last of March and the first of April. The absence of large numbers of darters from the riffles on April 19, 1953, was the result of cold weather. Although a few *E. caeruleum* were caught in pool A, they were much more common on larger riffles downstream.

In the spring, *E. blennioides* was distributed almost linearly along the narrow stream. Thus very few individuals were represented in the collections. This species was associated in the breeding season (April and early May) with the rubble riffles E, H, J, L and P, where the rocks had a heavy growth of *Cladophora,* upon which the eggs were deposited. The presence of the fish on plots B and R may be explained by the existence of a few scattered large rocks on those riffles. Plot P had a heavy growth of *Cladophora* in the spring of 1952 and *E. blennioides* was present. Near the beginning of the reproductive season in 1953, they were on Plot P, but disappeared during April and May. The presence of a crustal blue-green algal association, and the lack of *Cladophora,* are considered significant.

Etheostoma microperca was obtained in pools A and S and in the marginal vegetation of Station B, where the water flow was negligible.

Etheostoma flabellare was found on plots A, B, E, H, J, L, N, P, R, W and X. Nests were located under rocks only on E, H, J, L and P, but a few larger rocks were near or on the edges of plots B, N, R, W and X where they presumably might have spawned. Like *E. blennioides,* this species has an essentially linear distribution of territories on narrow rubble riffles. The distribution of the nests between plots H and J confirmed this.

The plots represented only a marginal spawning area for *E. nigrum* which bred more commonly in slower water in other parts of the stream system. This darter was present on riffles W and X and pools A and S in the breeding season, but no nests were found.

Etheostoma caeruleum and *E. spectabile* were the most common species that spawned on the plots. *Etheostoma caeruleum* bred on the rubble, coarse-gravel and fine-gravel riffles, whereas *E. spectabile* bred only on the fine-gravel riffles and on two coarse-gravel riffles. These two stations (W and X), where *E. spectabile* occurred in relatively small numbers, did not have any rocks over 50.8 mm in diameter, whereas the other coarse gravel plots (R and N) had from two to four rocks with a larger diameter than the above in the square-foot sample measured. This may explain the difference in species composition. Plot B contained small numbers of both species. The areas sampled represented only the peripheral habitat of *E. spectabile,* which, in the absence of *E. caeruleum,* is found in small headwater streams with a slow current over a bottom of sand and fine gravel. This ecological separation was noted by Trautman (1930) and was shown on the distribution maps of the two species by Gerking (1945). It was shown in a series of experiments by Winn (1956) that *E. spectabile* tended to lay eggs in finer gravel than *E. caeruleum* in the absence of any current.

Certain shifts in the proportions and absolute numbers of darters on riffles between the spring of 1952 and of 1953 are shown in Table 1, but it is difficult to determine the significance of these changes. They may be partly a function of the different dates on which the samples were taken. These may have been different points in the curve of a reproductive population on a riffle which increases to a peak or plateau and then decreases. In Figure 1, a dotted line near plot O represents the course of flow for the spring of 1951. It shifted, before the spring of 1952, to the channel represented by plot O. The 1951 riffle was about 1 m long and 1 m wide whereas the new riffle was about 5 m long and 1 m wide. This increased the reproductive area five-fold and the reproductive populations of *E. caeruleum* and *E. spectabile* at least five-fold.

Larimore, Pickering & Durham (1952) made an intensive fall survey of a creek in Illinois. They showed that *E. caeruleum* and *E. blennioides* were concentrated on the fast rocky riffles of the lower part of the stream, whereas *E. spectabile* and *E. flabellare* were more abundant in the upper, more sandy section. Furthermore, they found significant correlations between the above pairs of species and a negative correlation in other combinations. Because only a few areas were selected, no correlation coefficients could be worked out. However, in fall collections, adults of *E. flabellare* were found more often with *E. caeruleum* and *E. blennioides* on the riffles than either one was with *E. spectabile.* This discrepancy may mean that these workers did not consider the microhabitat or that they included young fishes, which were in a different habitat. It may be that small riffles not large enough for *E. caeruleum* or *E. blennioides* but large enough for *E. flabellare,* which goes farther into the headwaters, were present in the upper sandy sections. Any of these explanations could account for the differences of association, for these vary among the adults, the young and between the sexes.

Associates: The common non-darter associates found in the Mill Creek area, the Huron River

riffles, the tributary to the Saline River, the Saline River riffles, and Fleming Creek in the reproductive season were as follows: *Catostomus commersoni, Hypentelium nigricans, Hybopsis (Nocomis) biguttata, Pimephales (Hyborhynchus) notatus, Semotilus atromaculatus, Notropis cornutus, Rhinichthys atratulus, Campostoma anomalum, Noturus flavus* and *Cottus bairdi.* In Beer Creek the same minnows were present, except for the absence of *Hybopsis biguttata* and the presence of *Ericymba buccata. Lampetra (Entosphenus) lamottei* was present in Fleming Creek.

In contrast to the darters, most of the above species bred on the edges of pools and in slow raceways, especially over the gravel-covered areas. *Cottus bairdi,* which bred on some of the same riffles as *E. flabellare* laid eggs from the middle of March until the first of May, whereas *E. flabellare* started egg-laying about the first week of May. Thus there was little if any overlap in the time when the two species utilized the same riffles. *Noturus flavus* also used some of the riffles but did not lay its eggs until June and July (Greeley 1929: 174; 1934: 104), whereas the last few eggs laid by *E. flabellare* usually hatched by the second week of June. A few nests or egg deposition sites of *Campostoma anomalum, Catostomus commersoni* and *Lampetra lamottei* were built on the gravel riffles where *E. caeruleum* or *E. spectabile* bred. But the area used was usually very small and the major spawning of these non-darter species was in areas not employed by the darters. *Pimephales notatus* utilized some of the same undersides of rocks, boards and other objects as did *E. nigrum,* but the latter bred before the former species commenced in the first or middle of June. Hankinson (1919) recorded more overlap in the two reproductive seasons and a somewhat different habitat for these two species in Illinois.

In the lakes where *E. exile* and *E. microperca* spawned, the various non-darter species are spatially and temporally segregated from the darters. The centrarchids usually built their nests farther away from shore than where *E. exile* spawned. The minnows usually bred in the summer after the darters have spawned. In Whitmore Lake, *Fundulus notatus* was the only common species found over the same spawning area as *E. exile* and *E. microperca,* but the breeding seasons only partially overlapped. *Fundulus notatus* was also spatially separated, as it utilized the surface water almost exclusively (Carranza & Winn 1954), whereas the two species of darters protected the area on the bottom.

Several other stray fish associates were recorded in areas near breeding darter populations. Competition for space with any of these species was absent or negligible except possibly in peripheral situations. The utilization of the various microhabitats by darters and other fish apparently entails a minimum of competition. This is accomplished by both spatial and temporal isolation.

REPRODUCTIVE HABITS

MIGRATION

A variety of evidence indicates that the darters have a definite reproductive migration. This differs from Gerking's (1953) suggestion that many stream fishes live in a restricted area throughout their lifetime. After the reproductive season, most species leave the breeding grounds for deeper water or go downstream to a different habitat. In a few cases the migration covers a considerable distance. There are also limited data to indicate that the males as a group migrate shortly before the females. Abnormally cold weather can stop migration and even cause a reversal of its direction.

Percina caprodes migrated from the deeper waters to the shallow shoals in Douglas Lake and from the deep water of the lake or river into the outlet of Portage Lake. *Etheostoma microperca* and *E. exile* reacted similarly in both stream and lake habitats. The latter species migrated some distance from Sugarloaf Lake up the inlet stream. It was first recorded in the inlet when hundreds appeared on March 17, 1953 (John Williams, pers. comm.). No such spectacular appearance was recorded in 1954. Although most of the population was blocked by a weir they did not spawn on the favorable lake shoal as did the population in Whitmore Lake. Instead they bred in the 100 m of inlet stream under very crowded conditions. In Beer Creek, which was dry in the summer and fall, *H. maculatus, E. spectabile,* a few *E. blennioides,* and *E. nigrum* migrated several miles upstream from the permanent pools. A large migrating population was observed some distance below the breeding grounds in Honey Creek (tributary to Huron River about 3.5 mi northwest of Ann Arbor) on April 30, 1953. A few days later the majority had moved upstream. The occurrence, shortly before breeding, of *E. caeruleum, E. spectabile, E. microperca, E. blennioides* and *E. flabellare* on some riffles is shown in Table 1 for April and May. The small numbers of the latter two species are considered significant because of the large area they used for breeding. The disappearance of darters from riffles at the completion of the breeding season is shown in the same table. Lake (1936) recorded the migration of *E. flabellare* from swift water to riffle areas of moderate current. Individuals of *E. blennioides* migrated up streams that are dry part of the year. In Mill Creek below the dam, *E. blennioides* showed evidence of a migration. During the nonreproductive season some adult males were present on the riffle but in March and April there occurred, by conservative estimate, a five-fold increase in the number of large males. The wintering individuals on the riffle possibly tried to migrate upstream but were blocked by the dam.

Most species leave the breeding grounds after spawning, as shown for *H. copelandi* (Winn 1953). *Percina caprodes, E. exile, E. microperca* and *E. nigrum* went to the deeper parts of lakes and in some cases to the deeper parts of streams. *Etheostoma*

caeruleum, *E. blennioides* and *E. flabellare* went downstream to the larger, rubble-covered riffles. *Etheostoma caeruleum* completely left the gravel-covered riffles. *Etheostoma spectabile* moved to the deeper silt-covered pools, as did a few individuals of *E. caeruleum*. *Hadropterus maculatus* also left the breeding grounds probably to go to deeper pools. After the close of the reproductive period in 1954, *E. saxatile* was not seen or captured on its breeding-riffles or in the nearby pools. In Beer Creek, *E. spectabile*, *E. nigrum* and *H. maculatus* migrated at least down to the first permanent pools. Raney & Lachner (1939) were inclined to believe that *E. maculatum* moved but slightly to deeper parts of the same riffle during the winter months. That some individuals stayed in non-permanent pools was shown by the dead specimens of *E. spectabile* observed in several isolated pools with only a trace of water on July 13, 1952. No fish were recovered by digging in the damp gravel.

One other type of downstream movement which was not associated with reproductive activity was recorded for *E. caeruleum*, *E. blennioides* and *E. flabellare*. Certain small rubble riffles in the Saline River above the crossing of State Highway 11 became increasingly smaller as the water flow lessened during the summer. As a consequence, fewer adults of these three species were found on these riffles and it appears that they moved downstream to larger riffles. Trautman (1930) believed this to be true for *E. caeruleum* in Ohio. When the stream flow increased during the winter, from November to the onset of the breeding season, the reverse effect was observed until some adults were on or near the riffles used for breeding. On the contrary, Reed (MS.), in a study of marked darters (*E. blennioides*, *E. caeruleum*, *E. flabellare* and *E. zonale*), found that many individuals remained on the same riffle from June through September.

Several times, shortly after a migration had started, abnormally cold weather caused the darters to leave the breeding grounds. *E. caeruleum*, *E. spectabile*, *E. exile*, *E. blennioides* and *E. microperca* all usually started a migration from the middle to the end of March or the first of April in the Ann Arbor region. *Percina caprodes* migrated the latter part of March to the first of April in the same area. *Etheostoma flabellare* and *E. nigrum* migrated from the middle to the last of April. The variation of several weeks was due to the yearly differences in climatic factors, especially temperature. On April 19, 1953, the temperature dropped from the fifties to the low forties. At this time *E. caeruleum* and *E. spectabile* were absent from the gravel riffles, where they had started to congregate and breed earlier, but they were found in the pools. On the same date *E. exile* discontinued its migration up the inlet to Sugarloaf Lake. On April 22, 1951, the same phenomenon occurred in Fleming Creek; at this time the temperature drop was not more than 5°, but it was accompanied by rain and rushing turbid water. Climatic variations apparently determine whether the fish appear suddenly in large numbers on the spawning grounds or whether they slowly increase in numbers or even appear at all.

There are some data to show that males migrate slightly ahead of females. This seems to be true for *E. exile*, *P. caprodes* and probably the other darters as well as many other species of fishes. Lake (1936) found this to be true for *E. flabellare*. Also, the time of the spring migration varies considerably depending upon the seasonal temperatures.

REPRODUCTIVE PERIOD

In general the species which have the most complex spawning behavior and lay the fewest eggs breed later and have shorter mating seasons than the species which have the least complex breeding habits and lay more eggs. There is considerable interspecific and intraspecific variation in the reproductive periods. Some of the differences are seasonal, some are geographic, and others are presumably genetic. In the regions of southern Michigan and of Nashville, Tennessee, the more specialized breeders reproduce later in the spring. This is correlated with a slower, less voluminous flow of water which may be necessary for their advanced type of mating. The eggs are often laid earlier in the laboratory because of higher temperatures, and frequently a full complement is not laid under laboratory conditions.

In all species examined, the males ripened (when sperm are released externally on slight pressure) one to two weeks before the females, although this was difficult to ascertain in *E. nigrum* and *E. flabellare* because sperm cannot be readily stripped from them. The commencement of male territorial activity by these two species, shortly before the females contain ovulated eggs, probably indicates sexual maturation. It is only assumed that the males of *E. maculatum* and *E. saxatile* ripen first. Three other criteria which have been used as indicators of the reproductive period seem reliable when used together. One is the brilliant coloration of the males. This starts to develop in late fall and is often very intense several months before spawning occurs, although it may be most intense when reproduction starts. The intensity is almost impossible to measure by visual examination. It may be that the dark males of *E. nigrum* and *E. flabellare* indicate assumption of reproductive territorial behavior, although those of the latter species seem to darken somewhat earlier. Secondly, the presence of enlarged eggs does not necessarily indicate the start of spawning. The eggs form in late summer and continue to enlarge until the following spring, when they are laid. Near the beginning of the spawning season some eggs start to ripen, as evidenced by the change from opaqueness to transparency. When a certain number have ripened, which is variable according to the species and not ascertained in this study, egg-laying proceeds. Much further study is necessary to determine how many ripe eggs must be in the ovary in order to indicate when the first ones are laid. A third criterion, the

laying of eggs in the laboratory, involves multiple difficulties. The fish are removed from an environment where the temperature fluctuates considerably and are placed under more uniform conditions. The fish used for the present study were put in aquaria usually 5 to 12°C. higher than the daily maximum temperatures of the streams or lakes. Under these conditions they spawned 1-5 wks earlier than in the field.

The first presence of easily stripped eggs (after an undetermined number have ovulated) in all but a few species is usually a fair indication of when spawning starts, but it is not as reliable as continuous observation in the field. Such observations combined with most of the above criteria were used in this study. For most species it is believed that the time of egg laying is accurate within a week. For *E. nigrum* and *E. flabellare*, the only satisfactory standard was the appearance of eggs underneath the rocks. The collection of weekly or daily gravel samples from the riffles where *E. caeruleum* and *E. spectabile* spawn would be a satisfactory method, but it was not used here. The first presence of eggs in the algae is the best indication for *E. blennioides* (Fahy 1954, and present study). The lack of well formed eggs and the absence of males guarding eggs characterize the end of the reproductive period.

The general reproductive period for the various species, from the first to last laying of eggs, was as follows (Ann Arbor area unless otherwise stated): *P. caprodes*, from about the middle of June to about the third week of July in Douglas Lake, and from the first part of April until the last of May or the first part of June in the outlet of Portage Lake; *E. caeruleum* and *E. spectabile*, from the first of April to the first of June; *E. exile*, from the first two weeks of April to the last of May; *E. blennioides*, from the first of April to the last of May; *E. microperca*, from the middle of April to the first or middle of June; *H. copelandi*, from the last of June to the last of July in Cheboygan River, northern Michigan; *E. nigrum*, from the last week of April or the first week in May to the first of June; and *E. flabellare*, from the first week of May to the second week of June. *Etheostoma spectabile* became spent a few days to one week earlier than *E. caeruleum*. The reproductive period for *H. maculatus* was less clear. A few individuals bred during May in the outlet of Portage Lake. Petravicz (1938) said that spawning started in aquaria on March 19 and in the natural habitat on May 3. Females with a few ripe eggs left were collected in Perry Creek near Saginaw Bay, southeast of Tuscola, Tuscola County, Michigan on May 14, 1953, when females of *E. blennioides* were also partly spent and those of *E. caeruleum* had just started to spawn. *Etheostoma caeruleum*, *E. spectabile*, and *E. saxatile*, were at the peak of the breeding season the first week of April in Kentucky and Tennessee, whereas *E. blennioides* was almost spent. At the same time males of *E. flabellare* and *Ulocentra* sp. (Barren R.) in Tennessee were establishing territories, but it was not expected that the females would spawn for about a week. Raney & Lachner (1939) reported that *E. maculatum* spawns from the third or fourth week of May to about the third week in June.

A peak of spawning occurs in the middle of the reproductive period, as reported by Lake (1936) for *E. flabellare* and by Fahy (1954) for *E. blennioides*. The latter species also appeared to reach a climax during the time when the *Cladophora* or other suitable plants nearly reach maximum growth. The other species also exhibit a peak or plateau, but this was not studied in detail. All the females become gravid within a two week period and they all become spent within the last few weeks of the breeding season. In general, the yearling females of most or all the species ripen later than the older females.

Yearly variation in the reproductive season was not so great for the four years covered here (1951-1954) as was indicated by Fahy (1954) for 1948 through 1950 in New York. He gave the first and last egg-deposition dates for *E. blennioides* as follows: 1948, April 13 and June 12; 1949, April 27 and June 10; and 1950, May 5 and June 11. Most species from the Ann Arbor region spawned about one week or possibly two weeks earlier in 1953 than in 1952. Not enough information was available for 1951, but the season was about the same as in 1952. In 1954, March and the first half of April were considerably colder than during the three previous seasons, and the early-breeding species migrated and reproduced a varying number of weeks later. For instance, *P. caprodes* which arrived in the outlet of Portage Lake between March 22 and April 2, 1953, and started to breed the first week of April did not arrive until between May 9 and May 12 and did not breed until the second week of May, 1954. Other species were affected less drastically and others not at all. *Etheostoma caeruleum* and *E. spectabile* laid their first eggs between March 22 and April 2, 1953, and April 10 and 20, 1954. *Etheostoma blennioides* laid its first eggs between April 2 and 9, 1953 and April 21 and 25, 1954. The time of breeding for the above three species in the 1952 season was about halfway between that of the 1953 and 1954 seasons. *Etheostoma nigrum* and *E. flabellare* still started to lay eggs the first week of May. There was as much as 7-10 days difference in the onset of breeding of some local populations of one species. For instance, *E. exile* in Whitmore Lake bred at least one week later than the same species in the inlet to Sugarloaf Lake in 1953.

A sudden cold spell as well as turbulent silt-laden water caused by heavy rainfall, can temporarily slow or stop mating activity. Lake (1936) noted this latter effect on *E. flabellare*. The high water and silt may have stopped *E. caeruleum* from breeding in Fleming Creek, as mentioned under Migration. This is plausible, because vision is the most important sense used in sexual activities and possibly the only one used for food capture.

Although this investigation did not involve an analysis of geographic variation in behavior, regional differences in breeding activity were observed in several species. In Kentucky and Tennessee, *E. caeruleum* and *E. spectabile* were in the peak of spawning the first week in April, 1953, and *E. blennioides* was beyond its peak at a time when the same species were just beginning to spawn in the Ann Arbor area. *Etheostoma flabellare* was just ready to spawn the first week of April in Kentucky and Tennessee, whereas this species did not spawn until at least two weeks after that time in the Ann Arbor region. Only one set of *E. nigrum* eggs was found in a tributary to the Kentucky River on April 5, 1953, which was at least three weeks ahead of the time the first eggs were located in the Ann Arbor area. In the second situation a reversal in the order of breeding of several species was noted. In the Ann Arbor area, *P. caprodes* started to breed at the same time or earlier than *E. exile*, whereas *E. nigrum* started about a month later. They all finished their spring activities at about the same time. In Douglas Lake, several hundred miles farther north, both *E. exile* and *E. nigrum* finished breeding shortly before *P. caprodes* started. The explanation of this probably depends on the history of water temperatures for the spring in each region.

Species which manifest complex behavior and lay fewer eggs *(E. nigrum, E. maculatum* and *E. flabellare)* spawn approximately one month later than species with less complex spawning behavior which lay more eggs (Table 2). There is less time difference in the termination of the reproductive period. This later breeding period is correlated with considerably slower and less voluminous flow of water. The simplest interpretation is that the upside-down positions and other specialized spawning attitudes would be impossible to maintain under conditions of faster and greater flow. This view is strengthened by the fact that none of the species with more complex breeding habits spawns in the faster riffles but rather in raceways, pools and other slow-water areas. These areas have considerable flow in April which slows markedly from the last of April onward, with only minor, temporary setbacks because of rain. Also, Lake (1936) recorded a temporary discontinuation of reproduction for *E. flabellare* that was caused by heavy rainfall between May 2 and May 8. The shortness of the period in the more complex spawners is correlated with the fewer eggs laid.

Some evidence has been given to show that temperature plays an important role in the maturation of the gonads. It affects the reproductive season each year, stops reproduction at times, and probably influences geographic differences in time of breeding. Fish brought into the laboratory from temperatures of 10-17°C. and put into 21-24°C. ripened some eggs overnight which would not have matured until a later time in the field. When transferred from the field 2-5 wks before natural reproduction, the fish spawned within 1-3 days at temperatures often as much as 10-12° higher than in nature. Also, males kept in the laboratory from summer to the following spring had running milt by February. Although temperature is important for the maturation of the gonads, the possible effect of light has not been adequately excluded. Since this was written Hubbs & Strawn (1957) demonstrated experimentally that light did not play a role in maturation. It seems that under conditions of flood and sudden temperature drops, the maturation of eggs is slowed or temporarily stopped.

Territoriality and Range

A considerable number of papers have been written about territoriality in vertebrates, especially birds (Nice 1941), and it is well known in fishes (Breder 1934, 1940; Baerends & Baerends-van Roon 1950; Fabricius 1951; Gerking 1953; Pelkwijk & Tinbergen 1937). Noble's (1939) definition, that a territory is any defended area, is well established and accepted. As a group the darters exhibit marked differences in territorial behavior, grading from a simple pugnaciousness to a very strong defense of a given area. This behavior ranges from intraspecific protection, to a tendency towards interspecific protection and finally to a strong interspecific defense.

In the daytime the space occupied over the spawning grounds can be divided conveniently into the territory (male) or the reproductive range (female), the food range, and the escape range (Fig. 3). The characteristics of these divisions are as follows: *Territory or Reproductive Range*—A specific area, either moving or stationary, is defended by the male. The female has only a reproductive range, moving to and from the pools or deeper water to the riffles or shallow water to spawn periodically with the males within their territories. The males of the one species, *P. caprodes*, which form schools only have a reproductive range. *Food Range*—The male may move off the riffle or out of his territory for a brief period to feed. Typically this occurs only when no other males are trespassing. Males of *E. nigrum* and probably of *E. flabellare* seldom leave their territories to feed. Thus in the more specialized species the male's food range is more or less included in the territory. The female's food range coincides closely with the reproductive range, although she will move to special food areas such as those containing minnow eggs at the head of a riffle. The pool or deeper water is used by the female for feeding and resting after reproductive activities. She almost never feeds on the riffles or along the shore where the male territories are located. *Escape Range*—Males and females have the same escape range. In most species, if both sexes are on a riffle or along shore, they will flee to the pools or deeper water. There is a temporal difference in behavior between sexes, for the males usually return to the riffle or shore more quickly than do the females. Large mammals and birds are the most common stimuli for the escape reaction. The males of *E. nigrum*, *E. flabellare* and probably *E. macula-*

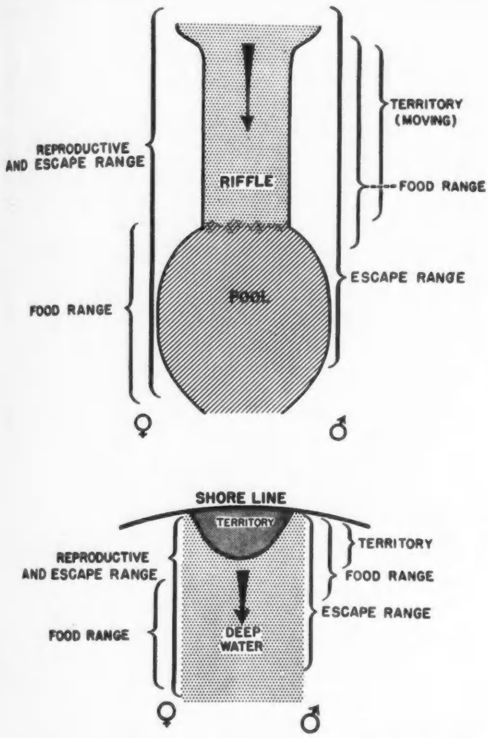

FIG. 3. A diagrammatic illustration of the territories and ranges of male and female darters. A moving territory on a riffle (*E. caeruleum, E. spectabile* and *E. saxatile*) is shown above and a stationary territory along the shore of a lake (*E. exile*) is shown below. In both, the reproductive and food ranges of the female cover similar areas although the center of each activity is in the opposite ends of the space utilized.

tum (Raney & Lachner 1939) only leave their territory under very great duress. Thus both the escape and food ranges are included in the male's territory.

There is no territorial defense at night. Both sexes remain relatively inactive on the bottom, making only compensatory movements to maintain equilibrium. Respiration is reduced Once a male of *E. nigrum* was observed moving slowly over its eggs immediately after lights were turned on.

With only minor deviations this description of day and night activities is characteristic of *P. caprodes* (stream), *H. maculatus, E. caeruleum, E. spectabile, E. saxatile, E. exile, E. blennioides, E. microperca, H. copelandi* and *E. (Ulocentra)* spp. In very large riffles, small pockets without males serve as pools for the females whereas those species which breed near the head of a riffle utilize the upper rather than the lower pool or the riffle itself. The males of *P. caprodes, H. maculatus, E. caeruleum, E. spectabile* and *E. saxatile* move freely over the whole riffle, whereas those of *E. exile, E. blennioides, E. microperca, H. copelandi* and *E. (Ulocentra)* spp., *E. nigrum, E. maculatum* and *E. flabellare* guard a stationary area. The males of the latter three species have coalesced the territory, food range and escape range essentially into one unit, the territory. In *E. nigrum*, the males will swim to deeper water only under extreme provocation, as when the rocks to which the eggs are attached are kicked vigorously. Thus the escape reaction and the region used for foraging change markedly from the less complex to the more complex forms. The other species which guard stationary areas form a more or less intermediate group. The females essentially maintain the same ranges in all the darters studied.

In the lake populations of *P. caprodes* the relationships of the territory, food range and escape range are similar except that the male reproductive school is equivalent to the male territory. The male school covers an area up to 30 m in length and parallel to the shore line, which is a much larger area than that covered by males with moving territories. The females feed in and escape into the deeper water beyond the male school. The males feed mostly over the breeding grounds and also escape into deeper water. This school formation is considered the most primitive reproductive type in darters.

It is unknown whether most species of darters confine their activities to one pool and one riffle during the entire reproductive season. However the males of *E. nigrum* and *E. flabellare* which care for their eggs appear to limit themselves to one territory if females are present. Also, it is not known whether the fishes return to the same pool and riffle the following year. One territory guarded by a male *H. copelandi* was maintained by the same individual throughout the breeding season, as is probably true for the males of all the species.

The territories maintained by the males of the various species studied can be summarized as follows (more detailed accounts were given by Winn 1955): *P. caprodes*—No territory is found in lake populations; males in a stream population, when following a female, make brief dashes at an approaching male when the latter comes closer than approximately 40 cm. No ritualized fighting occurs. Ritualized fighting or sham battles are terms used to denote the sexual fighting of males of the same species where no harm is inflicted on either opponent. *H. maculatus*—This species is similar to the stream population of *P. caprodes*. *E. caeruleum*—A male chases a male, when following a female, if the intruder approaches closer than about 30 cm. There is a tendency to restrict the territory to one spot when there is a large rock or depression in the gravel on the breeding grounds. Territories may be from 12 to 30 cm. in diameter. This and the following species exhibit ritualized fighting to some degree. *E. spectabile*—This species is similar to *E. caeruleum*. *E. saxatile*—The territory is similar to that of the above two species with the possibility that there is a little stronger tendency to guard stationary areas. *E. exile*—The male guards an area from 30 to 60 cm.

in diameter near the shore of a lake or at the margin of a stream. This and the remaining species have stationary territories. *E. blennioides*—Evidence indicates that a large stationary (laboratory evidence only) territory is held around large rocks covered with algae or moss. The territory appears to vary from 80 to 100 cm or more in diameter. *E. microperca*—Evidence indicates that a tendency is exhibited toward the protection of a small stationary area, roughly 30 cm in diameter, but that at times the area may be indefinite. *H. copelandi*—A territory about 90 cm in diameter with a rock in its center is guarded. *E. (Ulocentra)* sp. (Barren River)—A territory from 50 to over 100 cm is maintained about a large rock. It is presumed to be stationary from laboratory evidence. *E. (Ulocentra)* sp. (Green River)—The territory is similar to that of the above. Because the adult size is smaller, this form might be expected to have a slightly less extensive territory. *E. nigrum*—Distances from 25 cm to a much larger diameter around a rock or other suitable material are guarded. *E. maculatum*—Stationary territories have been recorded as more than 120 cm but with more observations it may be determined that they can be smaller. *E. flabellare*—Territories from diameters of 30 cm to usually much greater sizes are maintained around a rock.

Several types of territories displayed by the darters can be visualized. *Percina caprodes* and *H. maculatus* have completely "moving" territories which surround the female. This is considered to be the most primitive and least complex type. *Etheostoma caeruleum, E. spectabile,* and *E. saxatile* have moving territories, with a tendency to restrict them to specific areas. This restriction seems to depend on some large visual cue, such as a rock or a pit in the gravel. All the stationary kinds of territories have this large visual element. *Etheostoma exile* utilizes the shoreline or stream bank as a visual cue for the maintenance of the stationary territory. *Etheostoma blennioides, H. copelandi, E. (Ulocentra)* spp., *E. nigrum, E. maculatum* and *E. flabellare* have a restricted stationary territory with a large rock in the center. *Etheostoma microperca* utilizes plants in the delimitation of its territory, which may be indefinite at times. In streams of Texas, typical of the Gulf Coastal Plain, the rock habitat is scarce and a considerable number of darters representing different subgenera utilize plants for egg attachment (Clark Hubbs, pers. comm.) and presumably as the center of their defended area. In the stationary types, a propensity is exhibited toward an intimate use of a rock or plant for egg deposition.

Factors which determine the size and shape of territories in other fishes are population density, size of the fish, "distance of tolerance" characteristic of each species, topography of the substrate, and distribution of adequate spawning sites. These have been demonstrated by Baerends & Baerends-van Roon (1950), Fabricius (1951), and others. There are indications that all of these factors operate in darters, but most of them have not been studied in sufficient detail.

There is variation in the size of territories. In some cases only a small area is defended around the female *(E. caeruleum* and *E. spectabile).* Those species which scatter their eggs on the gravel with a rock as the center of the territory, on algae attached to a rock, or over the top of the rock, have large territories. The three species that lay a small mass of eggs under a rock *(E. nigrum, E. maculatum, E. flabellare)* establish small territories under crowded conditions in the field and in the laboratory. The first and third species set up two territories in tanks as small as 45 x 25 x 25 cm deep, whereas only one territory was established by *E. blennioides, H. copelandi,* and *E. (Ulocentra)* species in aquaria 91 x 46 x 37 cm deep. *Etheostoma nigrum, E. maculatum* and *E. flabellare* often had territories as widely separated in the field as do the other species because of a scattered distribution of adequate spawning sites. Only one male was dominant in tanks 45 x 25 x 25 cm and 50 x 30 x 30 cm deep for *E. caeruleum, E. spectabile, E. saxatile, E. exile* and *E. microperca.* These results are based on the introduction into the aquaria of only two pairs.

The moving territories have indefinite boundaries and the distance from which intruders provoke attacks by the defending male varies considerably. In the species with stationary territories the boundaries are more definite and become even more so in the three more specialized breeders (assumed for *E. maculatum*). None of the boundaries is as rigidly defined as that described for *Gasterosteus aculeatus* by Pelkwijk & Tinbergen (1937). When a male is in the spawning position other males may approach undisturbed, a feature characteristic of all the species. The intruders are not chased until the spawning act is completed.

Most of the territories are of irregular outline. The moving territories are approximately circular. The territory of *E. exile* forms roughly a half circle with the shoreline as the base. The territories of *E. nigrum* and *E. flabellare* radiate from the opening under the rock, which may be a narrow slit or around most of the rock. The shape is affected by the configuration and position of this nest rock. By an approach from the blind side, one male can usually get on top of the rock nest of another male without being challenged. The territories are essentially two-dimensional, with very little depth, except for those darters which lay their eggs on rocks or plants; these have a three-dimensional hump in the middle of the territory. The territory of *E. microperca* is three-dimensional in that the space occupied by the plants is also protected.

A protective mechanism is inherent in the stationary territory: males need contact with males as well as females in order to remain in a sexually active state of sufficient strength to maintain their territory. In the laboratory and probably in the field, if males of *E. nigrum* do not have eggs to guard

they will soon move from rock to rock. They clean off and protect each rock for a short time and then move on. As soon as eggs are laid, the males remain until they hatch. Intermittent wanderings of short duration were made from the territories by *H. copelandi, E. nigrum* and *E. flabellare.* Whether these movements are primarily for foraging, "attracting" females, or both is not known. It seems probable that these species also would shift their territories until established near a sexually active female.

A non-reproductive territory, comparable to the winter territory of birds (Nice 1941), is present in many species of darters. This was determined from laboratory observation and from the fact that adults were spaced well apart in the field. In one tank maintained throughout the summer and winter, *Etheostoma (Catonotus)* sp., from the Barren River, Kentucky and Tennessee, *E. flabellare* and *E. exile* maintained definite stationary areas although these were shifted during the year. To some extent these shifts depended on the varying positions of plants, growth of algae and place of feeding. All three species were very pugnacious in protecting their area, especially when food was added. In another tank, *E. spectabile* and *E. caeruleum* moved about much more but also exhibited a slight pugnaciousness which served as a spacing mechanism. Aquarium temperatures were more constant than those in the field but there is no reason to believe that this maintained the darters in a reproductive condition. Reaction to a mirror was very weak compared to the extreme agitation evoked during the breeding season. Most of the fish in both tanks were males, but the sex of every individual was not determined. *Etheostoma nigrum* failed to show a winter territory in the laboratory. This might have been due to the young stage of the fish used or they may not have such a territory because this species is often distributed in the non-reproductive season over uniform sandy and muddy areas, where there would not be any visual cues for establishing a territory.

Etheostoma spectabile, E. caeruleum, E. blennioides and *E. flabellare* were found scattered individually (mostly males) when an A. C. electric shocker was used to collect fish in the summer and fall. This is interpreted as a definite indication of some sort of a spacing mechanism which appears to be a form of territoriality. Thirty *E. blennioides* collected in Mill Creek on December 19, 1953, were widely separated. All were 25-600 cm apart, with 21 between 30 and 200 cm from their nearest neighbor. In the Saline River at highway 11, adults of *E. spectabile* and *E. caeruleum* were found to be separated usually by distances of 20 cm. or more in their respective habitats. Adults of *E. flabellare* were usually 50-100 cm apart under rocks on the riffles.

A non-reproductive and juvenile territory is well established for some coral-reef fishes (Breder 1949). Gerking (1953) established by indirect methods the probable presence of a non-reproductive territory in several centrarchids. I have observed late summer young-of-the-year *Micropterus salmoides* defending territories against each other. These facts, coupled with the information on the darters, tend to strengthen the view that non-reproductive territories in fishes are more common than published information now indicates. This type of territory is correlated with a strong reproductive territory in those species in which it is known. The knowledge that certain species maintain areas by aggressive behavior throughout the year is important in the understanding of the growth and size of populations (Gerking 1953).

Intraspecific and interspecific defense of the territory also is variable among the species. For the most part *P. caprodes, H. maculatus, E. caeruleum, E. spectabile, E. saxatile, E. exile, E. blennioides, E. microperca, H. copelandi* and *E. (Ulocentra)* spp. attack only individuals of their own species. Many of the above species as yet have not been tested with a wide variety of other forms. *Percina caprodes* sometimes exhibits pugnaciousness toward males of *H. maculatus*, and the two species are known to hybridize. When other species approach too closely, *E. saxatile, E. caeruleum* and *E. spectabile* sometimes erect their dorsal fins. Males of the last two species occasionally chase one another or even exhibit weak pugnacious behavior against other species in their winter territory. The two *Ulocentra* forms regarded each other's males as they did their own males in defense of the territory. In these two species and in *E. blennioides* there was a slight tendency to defend against other species. Males of *E. blennioides* sometimes attacked a male or even a female of *E. caeruleum*, but at other times they ignored them or even followed them as they did females of their own species. Even *E. exile* attacked other species when a winter territory was established in the laboratory. However, none of the above species ever attacked models, even when they were freshly dead males of their own species. Little is known about interspecific defense by *H. copelandi*, except that it did not chase or challenge *P. caprodes* which is a much larger darter. On the other hand *E. nigrum* and *E. flabellare* fight intensely against all species and even attack models which are about the same size. It is not known whether they would attack other fish much larger than themselves. Also, *E. flabellare* attacked other species when defending winter territories.

In all species of darters the pelvic, anal and caudal fins are held stiffly erect in a challenge or fight between two males. The head is often lowered and the erect caudal fin elevates the posterior region of the body when an intense fight ensues. Certain specific differences were noted in the manner of fighting. In *P. caprodes* and *H. maculatus* only a short movement towards an intruder sufficed to make him leave. The males of the other species, faced in opposite directions, displayed laterally, turned in a circle and made brief head butts at their opponent's caudal region until one fled with his fins depressed. In *E. nigrum* and *E. flabellare* the head butts are accompanied by attempts to bite the opponent. Once

dominance is established the superior male, with fins erect, dashes at the intruder who flees with relaxed fins. Also, in the natural habitat, two males with fins erect may move upstream beside each other.

The manner in which a male attacked his mirror image showed certain quantitative and qualitative differences. Most species attacked their images across a mirror 20 cm wide at the base. Several individuals of *H. maculatus* raced directly at the mirror while swimming a few centimeters above the bottom, but the reaction was not very intense. *Etheostoma caeruleum* moved parallel to the bottom of the mirror in a series of three dashes which formed small arcs, with the head often in contact with the mirror in the middle of each arc. In 5 minutes, one individual made 35 assaults, but only rarely was the mirror approached by a head-on dash. The body was slightly U-curved toward the mirror and the head was often directed slightly downward. *Etheostoma spectabile* and *E.* sp. (Barren River) reacted similarly, one individual of the latter species making 58 dashes along the mirror in 5 min. Two individuals of *E.* sp. (Green River) made 103 and 83 parallel spurts respectively along the mirror in two 5-min periods, and they normally made four arcs along the base of the mirror. The males of *E. saxatile* faced the mirror at right angles, bumping their snouts against it, but this may not have been the normal reaction. Such erratic reactions to the mirror were not amenable to quantification. Males of *E. blennioides* moved back and forth in front of the mirror with their snouts often in contact with it. Then at irregular intervals, with a flip of the caudal fin, they butted the mirror at a slight angle. In 5 min, two individuals made 4 and 9 butts respectively at the mirror and 99 and 89 movements, respectively, parallel to the mirror. The males of *E. exile* moved along the mirror slowly, darted almost straight at it and then swam slowly parallel to it. They sometimes rose off the bottom, pushing against the mirror. *Etheostoma microperca* males reacted at brief intervals to the mirror usually with straight dashes at their images. The males moved several centimeters away from the mirror and then back beside it again about 2 cm away. In two 5-min periods, one male made 55 and 60 movements approximately parallel to the mirror, and these included, respectively, 11 and 9 headlong assaults.

In most species the color pattern changed and the intensity of color increased after the male started to attack his image. The females and inferior males never attacked the mirror but either showed what might be termed an "exploratory" reaction or attempted to swim through it. Although occasionally a darter will bite an opponent or a model, this was never observed in nature or in quarters with sufficient area for flight. One characteristic reaction was observed in all the species: whenever a female approached a male at a rapid pace he first erected his dorsals and then lowered them. Initially, this behavior is presumably a response to movement; then if the approaching fish is a male, the fins remain erect, or if a female the fins are relaxed.

Dominance relations in the darter depend upon prior rights and size of the individuals. *Percina caprodes* is the only darter studied that forms schools. Of the other types of societies given by Baerends & Baerends-van Roon (1950), the dominated school, the dominated territorial school, and the "hierarchical" school are not represented in the darters. Many instances of the dominance of larger males were given by Winn (1958). Several times males of *E. caeruleum, E. blennioides, E. (Ulocentra)* spp., and *E. nigrum* were allowed to become dominant and then larger males were introduced. The smaller males sometimes remained dominant or the larger one became ascendant after a fight with the resident male. In the field or in more spacious surroundings, the efforts of the smaller established male would discourage the large intruder. Ordinarily the larger males are more successful in the primary institution of the territories, while the smaller males fight for the remaining areas. The intermediate-sized males of *E. caeruleum* and *E. spectabile* were quite often sexually more active in the laboratory and thus were dominant over larger fish. When the larger individuals became sexually active, as measured by their tendency to fight and to follow females, they became dominant over the males of intermediate size.

Noble (1938) pointed out that territorial behavior is correlated with sexual dimorphism. All darters exhibit sexual dimorphism to some extent. *Percina caprodes* and *H. maculatus* show less sexual dimorphism in color and have less well-developed territories than the other darters.

Several observations and experiments shed light onto some of the cues necessary for the maintenance of a territory. When a piece of tin with attached eggs attended by a male of *E. nigrum* was moved, the male remained in the same spot and returned when chased away (Adams & Hankinson 1928). When the tin was placed in a dip-net and lowered to the bottom near the male, he came under the net at once. This suggested to Atz (1940) that the male guards the place where the nest is located, not the eggs. An empty rock, occupied but not defended by a small male, was exchanged for a rock containing eggs which was guarded by a large male. The large male continued to move over the substitute empty rock but soon the male's activity decreased. The small male, on the other hand, increased his activities while caring for the eggs and successfully defended the area against the large male. This suggests that the eggs also stimulated movements under the rock and defensive activities. Longley (Longley & Hildebrand 1941) moved a *Strombus* shell containing eggs one yard away from the territory of a male *Pomacentrus leucostictus,* which continued to guard the original site.

Etheostoma blennioides, which is intermediate in behavioral complexity, needs a large tank and more

than one male near the onset of spawning in order to establish a territory. One male with one or more females will spawn normally but will exhibit no pugnacious behavior. In 14 experiments (aquaria 91 x 46 x 37 cm deep), one male was placed in a tank with two ripe females. Eight of the males were yearlings and six were two-year-olds. In all these experiments a mirror placed in the tank did not produce a fighting reaction. In 9 of the above setups a second male, that was smaller, the same size or larger than the first, was introduced after all the eggs were laid, and in no case was any territoriality or dominance exhibited. Spent females were not attacked in the above situations. Conversely, in fourteen additional experiments, in which two males and two females were placed in a tank at the same time, one male set up his territory, usually throughout the tank. The larger male chased the smaller one and the spent females (though less vigorously), and he readily attacked his mirror image. Aronson (1948) pointed out the importance of the social situation in studies on *Tilapia macrocephalus* where, when two females are together, one behaves much like a male. The above experiments with one and two males of *E. blennioides* showing the absence and presence of territorial behavior also illustrates the importance of the social conditions. The fact that *E. blennioides* establishes territories under certain spatial conditions and not under others (Winn 1958) indicates that the ecological conditions are also important. This may also be illustrated by lake and stream populations of *P. caprodes* if the differences in their reproductive habits are caused by the environment.

At one extreme from *E. blennioides* is the non-territorial lake population of *P. caprodes* which requires a large area over which to spawn and possibly needs constant contact with the males in the school for stimulation. *Etheostoma nigrum* is at the other extreme, for here the defense of the territory is evident in the absence of other males but not females of its own species. A single male in a tank reacted to his mirror image and attacked males that were introduced after all the eggs were laid (as demonstrated in two trials). Almost any moving object may also provide a stimulus for the males of *E. nigrum* while the presence of eggs may be the added stimulus necessary to keep the male in a condition for territorial defense.

The territorial society regulates the population size of darters in that males can fertilize and care for only a limited number of eggs. In this type of society there is always a reserve of males. The territory also serves as an area for undisturbed mating and enables the sexes to find each other. When the territorial structure is disrupted the population size is affected. *Etheostoma exile* was blocked from migrating up the inlet of Sugarloaf Lake and thus thousands were crowded in a 300-m stretch of stream. Territoriality and sex recognition completely broke down and this resulted in wasted energy and presumably a great loss of eggs. They did not utilize the nearby lake shoal which is very similar to that used by the same species in Whitmore Lake. It is quite apparent from this natural experiment that such a breakdown will bring the population to a lower level so that the natural population structure can be maintained. Moderately crowded laboratory conditions resemble this to a certain extent. On the other hand, certain populations of *E. nigrum* utilize peripheral unsuitable sites for reproduction.

In the darters, the more actively defended and better developed territories serve to protect the eggs from predation by other as well as their own species (*E. nigrum* and *E. flabellare*, etc.). Many species of fish defend their territories against other species, even non-piscine predators, although nest-site establishment is usually contested only with males of their own species. This is well known for some minnows, most if not all sunfishes, some darters, and sticklebacks (Raney 1940; Breder 1936; Atz 1940; Tinbergen 1951; and personal observations by the author on all four groups). In these examples the defense involves the laying of eggs in some sort of a nest, often in gravel and usually by a large species, where the eggs are vulnerable, especially to fish predation.

That territorial defense is intimately associated with reproduction is assured, but its relationship with the population and selection is obscure. The primary reason for the early selection of pugnacious behavior also remains obscure because other fishes are successful in the absence of a pronounced negative reaction to other individuals. Many of the functions ascribed to the territory are not achieved until after the territory has become highly specialized. Present function in specialized forms should be distinguished from the original selective force that starts a group to evolve pugnacious behavior. In fact, different selective forces may come into operation as primitive pugnacious behavior (such as that described for *P. caprodes* and *H. maculatus*) evolves into a complex, more specialized defense (characteristic of *E. nigrum* and *E. flabellare*).

Sexual Dimorphism and Sex Recognition

Various types of morphological and behavioral differences between the sexes, both slight and extreme, are exhibited by the darters. The morphological differences have not, in most cases, been related functionally to behavior. However, the correlations between the behavioral and morphological traits are strongly suggestive of the functional relationships. The major items of sexual dimorphism found in the breeding season are listed briefly below. Some of the information was taken from Fahy (1954), Gosline (1947), Lake (1936), J. J. Petravicz (1936), W. P. Petravicz (1938), Raney & Lachner (1939), Reeves (1907) and Reighard (1913).

Data on sexually dimorphic characters are presented in Table 3. On cursory examination, the fins of many species are found to be slightly larger in the male. Only the dorsals of *E. nigrum* and *E.*

TABLE 3. Sexual dimorphism of darters (*Percina, Hadropterus* and *Etheostoma*). Additional details are given in the text.

Species	Relative size of sexes	Male fins larger than female[a]	Female urogenital papillae	Breeding tubercles	Strikingly dimorphic structures
P. caprodes	Equal	A	Elongate, broadened, tube-like	None	None
H. maculatus	Equal	None	Elongate, broadened, tube-like	None	None
E. caeruleum	Male larger	A, D_1, P_1, P_2	Elongate, broadened, tube-like	None	None
E. spectabile	Male larger	A, D_1, P_1, P_2	Elongate, broadened, tube-like	None	None
E. saxatile	Male larger	A, P_2	Elongate, broadened, tube-like	On A and P_2 fins	None
E. exile	Female larger	A, D_1	Elongate, tube-like	None	None
E. blennioides	Male larger	A, D_1, P_1, P_2	Elongate, tube-like	None	None
E. microperca	Female larger	P_1, P_2	Elongate, tube-like	On P_2 fins	Extremely long P_2 with outer web of thickened skin, almost forms cup
H. copelandi	Male larger	A	Elongate, tube-like	None	None
E. (*Ulocentra*) sp. Barren R.	Male larger	A, D_1, P_2	Elongate, tube-like	None	None
E. (*Ulocentra*) sp. Green R.	Male larger	A, D_1, P_2	Elongate, tube-like	None	None
E. nigrum	Male larger	A, D_1, D_2, P_1, P_2	Flattened and flower-like	None	First 4 or 5 spines of D_1 with thickened opaque white tips
E. maculatum	Male larger	A, D_1, D_2, P_1, P_2	Flattened and flower-like	None	None
E. flabellare	Male larger	A, P_1, P_2	Flattened and flower-like	None	Spines of D_1 with orange, fleshy bulbs at tips

[a]A, anal fin D_1, first dorsal D_2, second dorsal P_1, pectorals P_2, pelvics

maculatum are noticeably enlarged. In most of the species the pelvic fins of the male had a slightly thickened outer margin. The color and body pattern are often strikingly different between the sexes. The male's body and fins are slightly blacker with a somewhat different body pattern than the female of *P. caprodes, H. copelandi,* and *H. maculatus.* The latter species can rapidly change the intensity and pattern of black and white coloration at any time of the year and does so frequently during the spawning act. The males of *E. caeruleum* and *E. spectabile* are a brilliant blue-green and orange with a different distribution of these colors in the two species whereas the females are a dull neutral-olivaceous with tinges of blue and orange. The male of *E. saxatile* is bright blue and the male of *E. exile* is red, red-orange and black with some green on the anal and pelvic fins whereas the females are not brightly colored. The male of *E. blennioides* is bright green with rufous-orange spots, whereas the female is brownish and light green. In *E. microperca* the dorsal, anal and pelvic fins are orange in the male and the female is neutral-colored. The male of *E. (Ulocentra)* sp., Barren R., is red and black with a bright green snout, whereas the female is black and white with a tinge of red. The color is the same for *E. (Ulocentra)* sp., Green R., but with a slight constant difference in pattern. The males of *E. nigrum* and *E. flabellare* are much blacker than the neutral gray or brown colored females. The male of *E. maculatum* has red spots and a blue-green coloration in contrast to the dull-colored female with only a tinge of the male's bright colors.

The male is larger than the female in all the species studied that have a well-developed territory, with the exception of *E. microperca* and *E. exile.* Sex recognition and a stationary territory were easily disrupted in those species. In *P. caprodes,* which spawns in schools or exhibits a very primitive, weakly developed pugnaciousness, and *H. maculatus,* which

also exhibits a primitive pugnaciousness, the sexes are of equal size. The males are smaller in *Perca flavescens* (Raney & Lachner 1943) and *Stizostedion vitreum* (Eschmeyer 1950). These two species spawn in large schools or other types of aggregations and they exhibit no pugnacious behavior. Raney & Lachner (1943) pointed out that a parallel situation is found in the Cyprinidae. A greater food consumption of the male of *E. blennioides* during the breeding season (Fahy 1954) is also correlated with larger size.

In the species which manifest pugnacious behavior to various degrees, the male has enlarged fins. The anal, pelvic and first dorsal fins exhibit this dimorphism, which is slight in most species. The sexes of *P. caprodes* and *H. maculatus*, which are of nearly equal size, show the least amount of sexual dimorphism in these features. Reighard (1920) pointed out that the fins of male catostomids are larger than those of the female and that these fish are non-pugnacious school spawners. In a few instances striking modifications are developed which are more readily related to behavior. The elongate cup-like pelvic fins of male *E. microperca* are caused by the bending inward of the large fleshy flap on the outer edge of these fins. The fins bear a resemblance to the disk caused by the fusion of the pelvics in the gobies. This modification probably helps the male maintain his position on the female during the spawning act. The males of *E. nigrum*, *E. maculatum*, and *E. flabellare* all exhibit striking modifications of the dorsal fins. In the first and third species the dorsals are used to clean an area on the under side of a rock before egg deposition and subsequently, to rub the eggs. This behavior has not been established for *E. maculatum*. In *E. flabellare*, the prominent fleshy bulbs at the tips of the spines of the first dorsal and the outer edge of the second dorsal are the only parts used to brush the eggs.

In general the shape of the female's urogenital papilla is related to the reproductive habits and is often a specific character. An elongate tube-like structure is typical of the gravel, plant and vertical rock spawners, whereas a flattened, flower-like and more intricate papilla is found in the complex inverted spawners (Tables 2 and 3). The papilla is most prominent during the spawning season.

The sporadic presence of breeding tubercles only on the anal and pelvic fins of a few species of darters is not readily understandable. Their function in *E. saxatile* and *E. microperca* may be stimulatory or they may aid in the maintenance of the spawning position, but other species without tubercles have similar habits and mating attitudes. Reighard (1920) thought that the pearl organs (breeding tubercles) in the suckers helped to maintain the mating position. The development of breeding tubercles varies in different groups of fishes, but they are quite often present on the fins or other parts of the fish that come in contact with the female during the spawning embrace or that touch other males in fighting.

There is a general correlation between territorial behavior and the degree of color and behavioral differences between the sexes. The males of the least dimorphic forms, *P. caprodes*, *H. maculatus*, and *E. microperca*, mount other males much more frequently than do those of the other species.

On the basis of preliminary study only, the following system of sex recognition is postulated: (A) males of *P. caprodes* recognize each other by their behavior in streams but not at all in lakes; males of *E. caeruleum* and *E. blennioides* recognize males by their bright hues and movements; males of *E. nigrum* and *E. flabellare* attack males on the basis of color and movements, but also attack other objects that lack female characteristics: (B) in *P. caprodes*, *E. caeruleum*, *E. blennioides* and *E. (Ulocentra)* spp., males follow females because they react to particular movements of the females; in *E. nigrum* and *E. flabellare* males recognize females by their complex behavior; (C) males mount females on the basis of a behavioral trait such as stopping, gravel-burying or assuming some other particular attitude; and (D) males and females in the copulatory position are tactually stimulated to start vibrations which are accompanied by the extrusion of eggs and sperm, except that *E. nigrum* probably releases sperm only when the pair moves in the inverted position on the underside of a rock.

The following experiments suggest some of the mechanisms and possible evolutionary aspects of sex recognition:

No. 1.—Freshly dead males and females of *E. caeruleum*, *E. blennioides* and *E. (Ulocentra)* sp., either free or attached to a string and moved, were placed in tanks that contained live individuals of their respective species. Males did not attack males or try to mount females except in two out of 20 trials. A dead female of *E. blennioides* was watched and nudged by a male and a dead male placed on the back of a dead female was attacked once. After a dead female of *E. (Ulocentra)* sp. was jerked up the side of a rock several times, it was mounted by a male. Males briefly erected their dorsal fins when any object was dragged across the bottom, but this was considered to be a surprise reaction rather than the recognition of any specific sexual stimulus. After the brief fin erection, the fish usually ignored these dead or inanimate objects or dashed away from them. This same reaction resulted from the use of models of these three species.

No. 2.—The males of all species except *P. caprodes*, which was not tested, vigorously attacked their mirror images and assailed males but not females in closed vials.

No. 3.—Males of *H. maculatus* attacked only their own species in a tank that also contained *E. caeruleum*, *E. flabellare* and *E. microperca*.

No. 4.—Reighard (1913) was able to get males of *P. caprodes* from a lake population to mount dead males by moving them across the sand and then stopping them. In the field a male followed either

sex that swam away from the school. This was often a male and when it stopped, the "following" male mounted. Since the male that was mounted did not react like a female (swam away instead), no synchronous vibration was performed. Whether the female initiates the vibration is not known. Stream populations of *P. caprodes* have not been studied sufficiently to determine what added stimulus causes males to attack males, but behavior may still be the basis of sex recognition.

No. 5.—Males of *E. caeruleum* only attacked an anesthetized male when it started to move. They also attacked a male which moved in a vial but halted when it stopped moving. They assaulted a male in a brown vial, which changed the blue-green to a greener color, but did not attack a male in a colorless vial covered with red cellophane, which made the blue appear black. There appeared to be no reduction in visibility as compared to the brown vial. Red cellophane covering one side of a vial prevented an attack from that side. On the uncovered side the imprisoned male looked blue against a red background and was attacked.

No. 6.—There appeared to be no definite sexual reactions between *E. spectabile* and *E. caeruleum*. Females, placed with males of the other species, buried themselves in the gravel, but the males did not mount, although sometimes they advanced toward the female or followed her for a while. Males ordinarily did not chase males of the other species. Once a yearling male of *E. spectabile* was chased when he approached a male of *E. caeruleum* that was closely following an active female of the latter species. No reactions between the two species were noted in the field when both were abundant on the same riffle. A male *E. spectabile* in a vial was not attacked by a male *E. caeruleum*, and vice versa.

No. 7.—A male of *E. (Ulocentra)* sp., Barren River, swam up the side of a tank as though attempting to get out, then drifted slowly down to the bottom where he landed on top of another male that he could not see. At the precise moment the male landed, he vibrated vigorously before swimming off the male underneath.

No. 8.—A male of *E. (Ulocentra)* sp., Barren River, circled a male of *E. exile* in a fighting pose, briefly erected his dorsals at a recuperating urethaned male of *E. caeruleum*, followed another recovering urethaned male and female of *E. caeruleum* as he would his own female, and once tried to mount a male of *E. exile*. The females of *E. (Ulocentra)* sp. showed no particular reaction to the above two species. A male of *E. (Ulocentra)* sp. following a female of *E. caeruleum* briefly challenged a male of *E. caeruleum* who landed on her.

No. 9.—A dominant male of *E. blennioides* followed a less bright male who was moving, half buried, in the alga, but at all other times the light-colored male was chased by the dominant male.

No. 10.—Males of *E. blennioides* attacked males of their own species placed in closed vials but ceased when the imprisoned fish no longer moved. In one experiment a dying male was attacked until he succumbed, at which time both a male and a female bit his pectoral fin. Twenty times, recuperating urethaned or anoxic males and females of *E. caeruleum* were followed and frequently nudged by males of *E. blennioides* as though they were their own females. A spent female of *E. caeruleum* was attacked several times, and once a male of the same species was attacked. One female of *E. caeruleum* swam up on the alga where a male of *E. blennioides* mounted her, but she dashed away. Sometimes when a female of *E. caeruleum* recuperated from anesthesia, she dashed away from approaching large males of *E. blennioides*, but at other times she moved forward as though to attract the male. The male of *E. caeruleum* also sometimes dashed away. A few times a male of *E. caeruleum* attacked a yearling male of *E. blennioides*.

No. 11.—After the dorsal fins were removed from a dominant male of *E. blennioides*, he no longer fought his mirror image.

No. 12.—All dead males, females and many other moving objects were usually attacked by a territorial male of *E. nigrum*. Ripe females of *E. nigrum* in vials, as well as other males and females, were readily attacked. If the objects were not moved, they were finally ignored by the territorial male. A dead, ripe female was moved jerkily toward a territorial male for 22 trials. It was attacked 10 times, he bit at it briefly and then turned over under the rock 10 times, and twice he merely went under the rock and inverted. When a dead male was used the results were the same except that the last reaction did not occur. Sometimes a dead male or female put upside down under the rock was not attacked. Live ripe females which approached the nest were almost never attacked but instead were greeted by only a brief erection of the male's dorsals. In several experiments with *E. flabellare*, Lake (1936) noted the following behavior: a dead male on a wire was attacked; a jerkily moved dead female was poked, but when the model did the same to the male he let the model remain in the territory; a jerkily moved dead female introduced upside down was not bitten, but instead the male assumed the spawning position several times beside it; a dead male upside down was not attacked but the spawning position was not evoked.

No. 13.—Males of *E. microperca* often mounted males of the same species but with few exceptions all the other species were not observed to do so (species observations in Winn 1955).

Particular movements and positions are most important in the recognition of both males and females in the darters. Failure to attack dead or immobile males and the lack of response to dead females is strongly indicative of this (experiments 1 and 5). Breathing movements alone are not sufficient to provoke an attack (5). Sex recognition depends upon visual cues, as is shown in experiment 2 and by the failure to attack anesthetized males.

The ability of males to recognize one another appears to change considerably as sexual dimorphism becomes marked and other traits evolve. In lake populations of *P. caprodes*, a species with little sexual dimorphism, there is no evidence that males recognize each other, as shown in part by the experiments performed by Reighard (4) and by the fact that males are not attacked. Possibly both movement and color pattern enable males of *H. maculatus* to identify each other (3). Sex recognition is weak in *E. microperca* and, at times, in *E. exile* (Winn 1958) for males often mounted males under crowded conditions. The males of the other darters were never observed to mount a male even under crowded conditions. *Etheostoma blennioides* and *E. caeruleum* recognize their own males by color, pattern and movement, although there is an incipient tendency to attack other male darters. *Etheostoma nigrum* and *E. flabellare* attack all species, and it is possible that they no longer recognize their own males as such. Ritualized fights between males may occur because the territories are in contact and they try to establish territories in the same nesting sites. Other species leave when attacked. The erection of the fins and the elevation of the body off the substrate may be important male characteristics. The significance of the blackened coloration of *E. nigrum* and *E. flabellare* is unknown, since territorial males attacked ripe dead females attached to a wire as intensely as blackened males introduced in the same manner.

Male recognition of ripe females can be divided into three reactions, the "following," "mounting," and "quivering" reactions as discussed in more detail under the spawning act.

It is not clear exactly which characteristics cause a "following" reaction but they do not appear to be very specific. Males of *P. caprodes* are often followed by their own males (4), or males and females of other species are often followed as long as they do not exhibit male characteristics of their own species (6, 8, 9, 10); or the two sexes are not attacked if they move directly and jerkily into the territory (12). Thus almost any bottom-swimming fish of the proper size may be followed. Possibly low posture of the female, with her belly region touching the substrate, is significant, because spent females are quite often chased. The frequent "following" and "mounting" of males by males of their own species (4 and 13) is bisexual behavior in the sense defined by Beach (1944). This behavior in the darters seems to be caused in the least dimorphic forms by a lack of distinct behavioral differences. This is especially so in *P. caprodes* where the males mount other males which have exhibited the normal female behavior of swimming away from the male school and then stopping.

In *E. nigrum* and *E. flabellare* the female's jerky entrance into the territory and the upside-down position appear to be recognizable female characteristics (12). Why females are not usually attacked inside the boundary, whereas males are, is not clear, but perhaps the jerky movements and low posture account for the different reaction.

Adequate proof of the significance of the position of the female, such as stopping in a horizontal position or at an acute angle, gravel burying, or moving on alga, in the elicitation of the male mounting response is afforded by the many observations where a female being followed was deserted for another female that was in the characteristic position of the species. There is additional evidence for the significance of particular postures in the stimulation of the male mounting reaction in experiment 10, where a female of *E. caeruleum* swam onto the alga and was mounted by a male of *E. blennioides*.

Finally, the "quivering" response of the male on the female is tactually stimulated. Experiment 7, where a male accidentally landed on and vibrated with another male, favors this view.

In general, the evolution of sex recognition in the darters has involved more specific and complicated movements of the female. Early in evolution the mounting response was evoked when the female merely stopped in a horizontal position in species with slight morphological sexual dimorphism and weak sex recognition. Later, with more pronounced morphological dimorphism and efficient sex recognition, burying movements, stopping at acute angles on certain materials, and the upside-down positions were evolved. In general, differences in movement have evolved along with increased sexual dimorphism, with the former as female and the latter as male recognition marks (see Table 2). Also, the territory increases in complexity and the male becomes larger than the female. Only the two species which lay their eggs on debris and plants *(E. exile* and *E. microperca)* do not follow this exactly. In both, the female is larger. *Etheostoma microperca* has a variously developed territory, poor sex recognition, and moderate morphological sexual dimorphism. *Etheostoma exile* is markedly dimorphic and sex recognition is usually strong, but under certain conditions males also mount males. However, on the whole, there is a very close parallelism between morphology and behavior in the various species of darters.

There is a lack of evidence to indicate that females recognize males of their own species, although female courtship behavior is described. However, the females of *E. caeruleum* and *E. blennioides* also nudged and moved around males of other species. The escape reaction sometimes exhibited by females of *E. caeruleum* toward large males of *E. blennioides* (10) is interpreted as a response toward a large fish and not as a failure to recognize their own male.

Spent females are often chased by territorial males of *E. caeruleum*, *E. blennioides*, etc., but the behavior and body shape which may elicit the reaction is less clear. One possibility is that this is a negative reaction of the spent female to an approaching fish. Thus, she retreats and this action stimulates the male to chase her as he would a rapidly withdrawing male.

Sexual isolation is complete between most species

of darters with diverse habits and forms and is accomplished by behavioral, ecological and genetical means. However, *E. caeruleum* and *E. spectabile* breed on some of the same riffles, exhibit no observable differences in reproductive behavior, and are extremely similar morphologically except for the male breeding colors. Isolation for some obscure reason is essentially complete because males of neither species were observed to mount the females of the other species. The males and females of the allopatric forms of *E. (Ulocentra)* sp. which did not exhibit any observable differences in behavior treated each other as if they were the same species.

Courtship and Spawning

There is little behavior in the darters that can truly be designated as courtship, at least of a very complicated kind. If courtship is defined as pre-spawning activities between male and female, then the recognition of the female by the male and, as a consequence, his following her, is the simplest type of courtship. The consequent movement by the female which stimulates the male to mount is also considered part of the courtship.

In both the field and laboratory, males of *E. caeruleum* and *E. spectabile* were observed at times to lay their heads against the body of the female when she stopped on the gravel. Whether this behavior is stimulatory or not is unknown. Several times the females of *E. caeruleum, E. spectabile, E. blennioides* and *E. (Ulocentra)* spp., which appeared ready to spawn, made movements toward unresponsive males in aquaria. The females swam to a spawning site but returned to the inactive males and swam around, in front of, over and into them. This behavior appeared to activate the male into following the female to spawn. These activities of the females were observed only in aquaria. Their function may be to synchronize by stimulation the spawning act in time of stress.

The more complex behavior of *E. nigrum* and *E. flabellare* contains several other elements which are included under courtship. The male of both species often dashes back under his rock in the presence of a female and performs rapid movements where the eggs will be laid. These movements may "attract" the female. In aquaria, all the females (2-4 females and 2 males) spawn with the more active males, which seems to support this idea. The nudges of the male against a female under a rock could be regarded as courtship, but it probably is better to consider this behavior as part of the spawning act.

In more detail, reactions between the male and the female can be conveniently divided into the "following," "mounting" and "quivering" reactions. The first reaction is self-explanatory; the second refers to the movement by which the male mounts the female; and the third is a simultaneous vibration of both sexes concomitant with the laying of the eggs and their fertilization. These divisions are not satisfactory for *E. nigrum* and *E. flabellare.*

The females stay in pools or deeper waters until they are ready to spawn, when they move into the area where numerous males guard their territories. A male with a moving territory follows a female over the riffle; if a stationary territory is maintained, following occurs only in his guarded area. Females of other species are rarely followed because the behavior necessary to provoke a male to pursue them is absent. The "following" reaction also involves a "leading" reaction in that the female precedes the male to the material upon which the eggs are to be deposited.

After the "following" reaction takes place in the horizontal and vertical spawners, a particular posture of the female stimulates the male to carry out the "mounting" reaction where he assumes a position on top of her (Fig. 4). In *P. caprodes* (stream and lake) *H. maculatus, H. copelandi,* and *E. saxatile,* this reaction is evoked when the female stops in a horizontal position on the sand or gravel within sight of a male, whereas the female of *E. exile* halts in a horizontal to an acute position. In *E. caeruleum* and *E. spectabile,* the female partially buries herself in the gravel. This act immediately stimulates the male to assume the mounted position. However, when a male appears highly active beforehand, he will occasionally start to mount a female before the gravel-burying stimulus is given, but she usually darts away. This is also true for the other species. This buried position keeps the pair stationary because if a female performs the gravel-burying movements on slate and the male mounts, the vibrating pair shoot forward. In *E. blennioides* a few abrupt movements on the alga by the female stimulate the male to mount. Normally, if the female stops at a strongly acute to obtuse angle, this stimulates the male to assume the mounting position in *E. (Ulocentra)* spp. and *E. microperca.* The nature of the substrate used for egg deposition is apparently of consequence to the female, but not the male, although the male's territories must center around the proper objects to insure successful reproduction. Breder (1940) also thought that the females of *Lepomis gibbosus* selected the egg-laying area.

In the horizontal and vertical spawners the mutual release of the eggs and sperm is accomplished soon after the pair starts rapid vibrations which are stimulated by a simple tactile response of the male on the female. This is true for all the species except possibly the two discussed below. Observations indicate that either sex can initiate the vibrations or that they can be produced simultaneously. Females of most species can lay eggs by themselves but the vibrations that accompany this are not as rapid as when a male takes part. When a pair is in the mounted position the completion of this act takes precedence over male pugnacious behavior. In all species in the laboratory, a male intruder can approach close to the spawning pair without being chased, but he is immediately attacked after the mating act is completed.

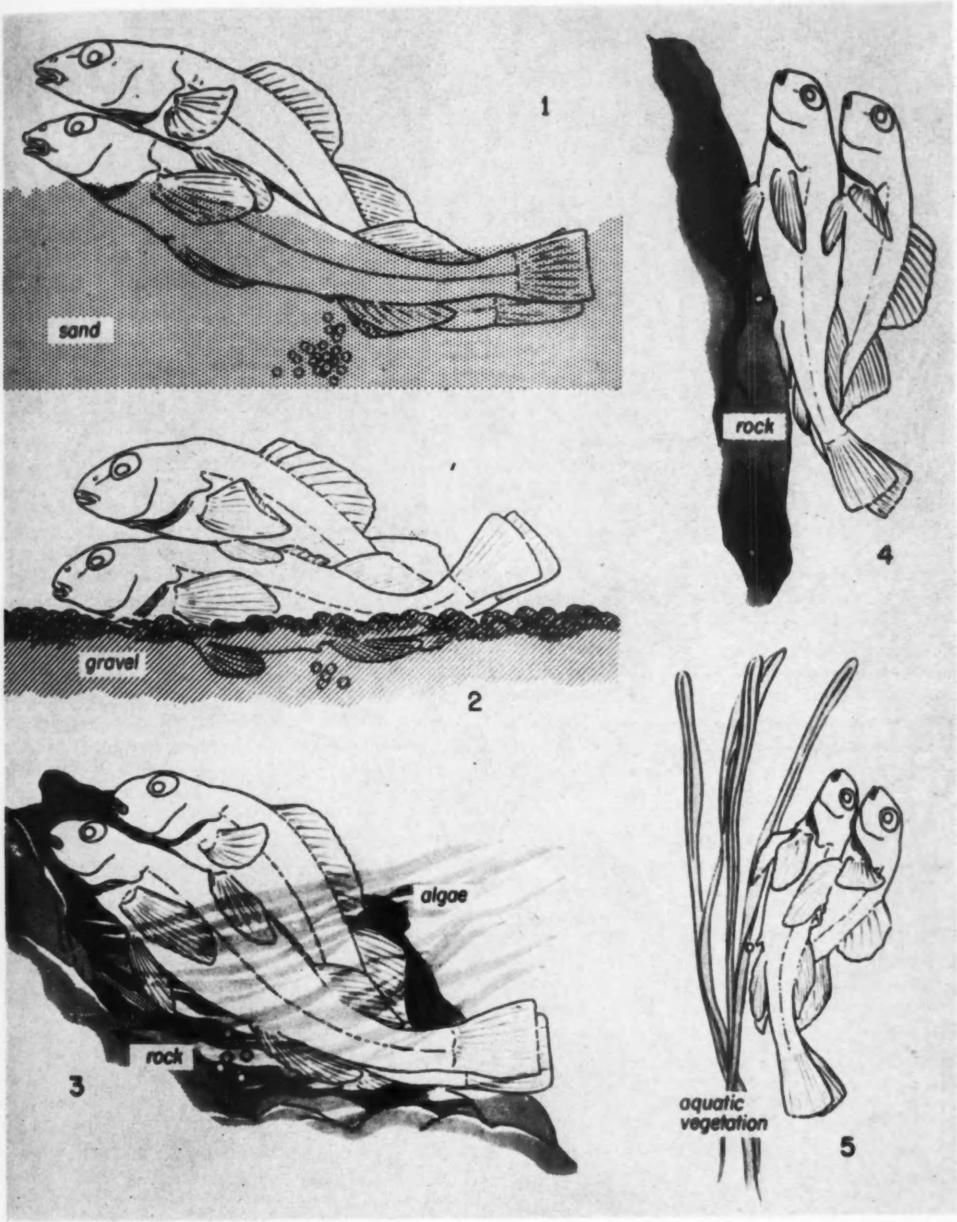

FIG. 4. The spawning position of some darters. 1. *P. caprodes*. 2. *E. caeruleum* (used as the type), *E. spectabile*, *E. saxatile*, *H. maculatus*, and *H. copelandi*. The mounted position of the sexes of *E. exile* is similar but the pair spawns on fibrous hard mud banks. 3. *E. blennioides*. 4. *E.* (*Ulocentra*) spp. 5. *E. microperca*.

The reproductive behavior of *E. flabellare* and *E. nigrum* exhibits conspicuous deviations from the mechanisms described above. The simple "following," "mounting" and "quivering" reactions are accomplished in a more complex manner. This is a related, if not a direct, result of the fact that the male-on-female positions cannot be maintained in the inverted horizontal position (see below and Fig. 5). The simple "following" reaction is modified. When a female enters a male's territory he typically comes out to meet her and swims in advance to the rock nest. Then the males of *E. flabellare* and *E. nigrum*, the latter upside down, swim rapidly around under the rock as though to attract the female. The female

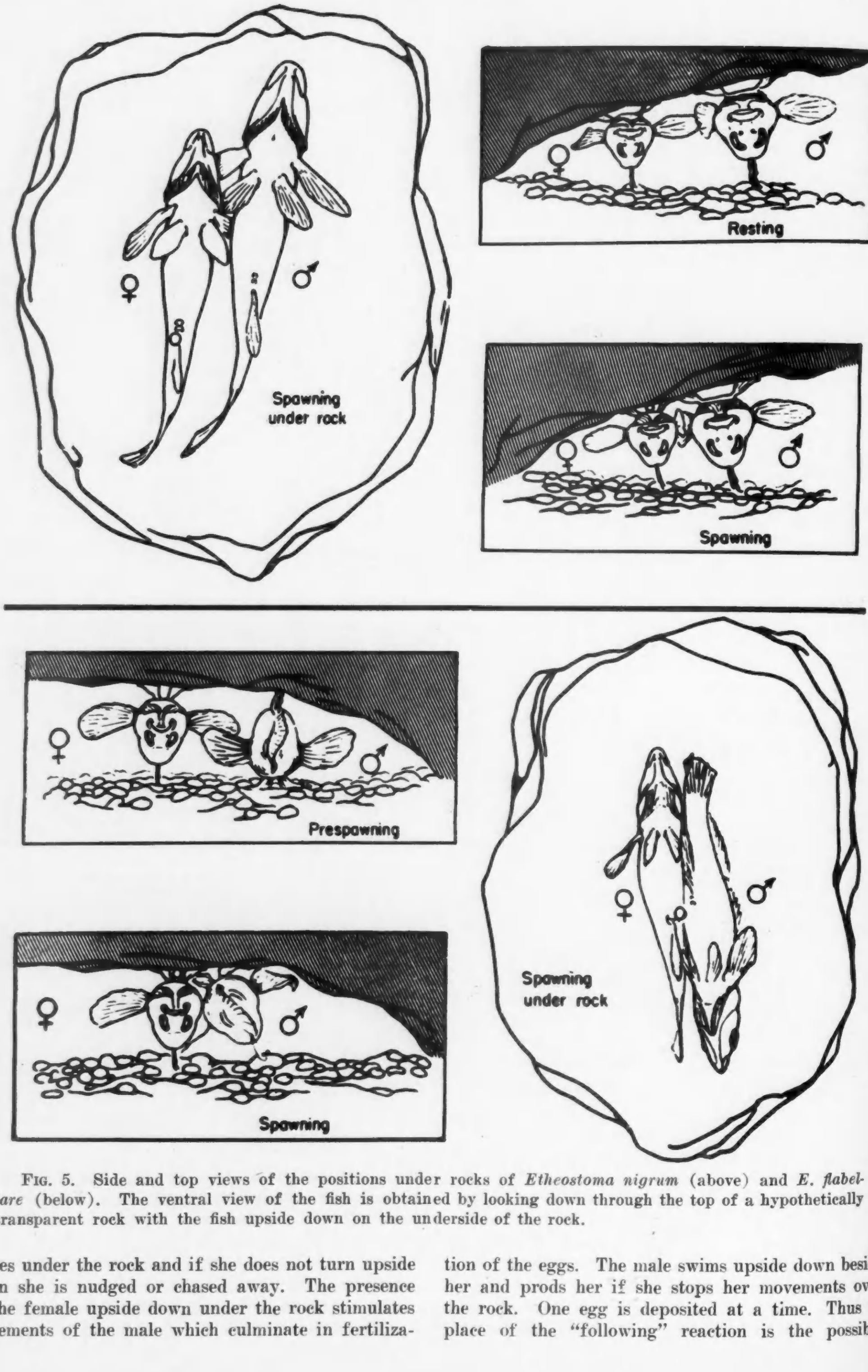

FIG. 5. Side and top views of the positions under rocks of *Etheostoma nigrum* (above) and *E. flabellare* (below). The ventral view of the fish is obtained by looking down through the top of a hypothetically transparent rock with the fish upside down on the underside of the rock.

moves under the rock and if she does not turn upside down she is nudged or chased away. The presence of the female upside down under the rock stimulates movements of the male which culminate in fertilization of the eggs. The male swims upside down beside her and prods her if she stops her movements over the rock. One egg is deposited at a time. Thus in place of the "following" reaction is the possible

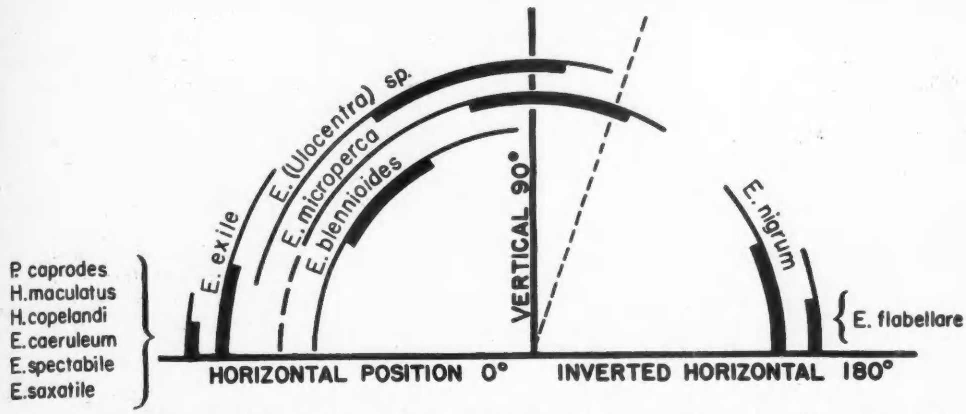

FIG. 6. Approximate variation in the positional relationship of the spawning pair, with respect to the substrate, in thirteen species of darters. These positions are shown in figs. 4 and 5. The heavy sections of the lines indicate what appeared to be the most common position for the given species. The dashed line represents a theoretical obtuse angle near which a special structure or a new mounted position is necessary for successful spawning.

attraction of the female by the rapid cleaning movements of the male under the rock where the eggs are to be deposited. The male prods the side of the female in *E. nigrum* or the caudal peduncle in *E. flabellare* and this action stimulates the female to move constantly and to lay eggs. Both sexes of *E. flabellare* vibrate slightly when the single egg is laid and fertilized. It appears that the vibration is initiated by the female and that this stimulates the male to flip on his side, vibrate and emit sperm. It may also be that the movements of the female under the rock excite her into a condition for egg laying. This fertilization act is brought about by a tactile stimulation. A chemical response cannot be completely ruled out, but a visual response to the egg is not feasible because the male is not in a position to see it. The egg is liberated shortly before or after the male turns over and releases sperm. In *E. nigrum* it is less clear when the male fertilizes the eggs. It is assumed that he excites the female to spawn by prodding her with his snout, and the female usually does not vibrate or exhibits only a brief trembling. It is possible that the upside-down movements of the female stimulates the male to release a small number of sperm intermittently. He covers the total area on which she lays eggs. On the other hand, in the horizontal spawners, a considerable amount of sperm is emitted at one vibration to insure the fertilization of the eggs before they are buried in the gravel. Thus an excess of sperm occurs in all behavioral types, but the loss is minimized by integration of the behavior of the two sexes.

The movements of the males under the rocks serve four purposes: to clean off the rock for egg deposition; to attract females; to keep the females and male together for egg-laying and fertilization; and to clean and aerate the eggs after they are laid.

The spawning position among the various species of darters varies from the normal horizontal position through a 180° arc to the upside-down or inverted horizontal position (Figs. 4, 5 and 6). Thus the position may be horizontal, acute, vertical, obtuse or inverted horizontal. The variability of these attitudes is based on laboratory and, where available, field observations. *Percina caprodes, H. maculatus, H. copelandi, E. spectabile, E. caeruleum* and *E. saxatile* all spawn in the upright horizontal position. This is referred to as the normal attitude. The position varies in *E. exile* from the horizontal (0°) to an acute angle less than 45 degrees; *E. blennioides* spawns from the horizontal to a vertical (90°) angle, most frequently at a 45° angle in the laboratory; *E. microperca* spawns from an acute to a slightly obtuse angle, usually in a nearly vertical position. *Etheostoma (Ulocentra)* spp. (Barren R. and Green R. forms) spawn in a horizontal position to a slightly obtuse angle, with the nearly vertical position the most frequent. In *E. flabellare* and *E. nigrum* both sexes are in the inverted horizontal position (180°), although in *E. flabellare* the prespawning position of the male is horizontal (Fig. 5).

The males of eleven species of darters maintain a position, described earlier, on the back of the female, until the pair spawns at anywhere from a horizontal to an obtuse angle (Fig. 6, also Figs. 4 and 5). Then a striking change takes place. The male fertilizes the eggs in a position beside the female in two species *(E. nigrum* and *E. flabellare)*. It is postulated that this change is the result of physical factors. The normal spawning position is made possible by the force of gravity, but in the inverted horizontal position, the negative effect of this force prevents the male from pressing against the female in a rigid embrace. The fact that males of *E. microperca* have developed special flaps on their pelvic fins strengthens this explanation, for these structures may be necessary to maintain the male in a position atop the female at an obtuse angle. *Etheostoma (Ulo-*

centra) spp., which have not developed any special structures, also spawn up to a slightly obtuse angle, but this takes place against rocks which form a solid base. If the modified pelvics of *E. microperca* are correlated with spawning against movable plants, then the critical angle when the mounted position changes should be more obtuse than shown in Fig. 6. The pectoral fins of the males of *E. nigrum* support them in an upside-down position in which attitude they clean the rocks and rub and fertilize the eggs. It seems likely that the force of the pectoral fins cannot overcome sufficiently the negative effect of gravity in order to maintain pressure against the female in the inverted horizontal position. The selection by *E. flabellare* of a space under a rock high enough for only one individual necessarily precludes the position of the male on the female's back. However, it may have been this effect of gravity that permitted *E. flabellare* to utilize such a nesting site, excluding other selective factors. If the normal male-on-female position could have been maintained it might have been allowed for in the selection of a nest site.

Certain other aspects of the spawning act show a trend from the simple to the more complex spawners (Table 2). In general, *P. caprodes* and presumably *H. maculatus* lay more than 10 eggs in one spawning act. *Etheostoma caeruleum, E. spectabile, E. saxatile, E. exile, E. blennioides* and *H. copelandi* lay approximately 3-10 eggs at a time. There is not enough data to indicate any trend within the group. *Etheostoma microperca,* a vertical plant spawner, *E. (Ulocentra)* spp., *E. nigrum* and *E. flabellare,* all vertical or inverted rock spawners, lay a single egg at a time. There is a correlation between the number of eggs laid in one spawning act and the number which can be readily stripped from a female. When stripped, *P. caprodes* releases a great many eggs, whereas *E. caeruleum, E. spectabile, E. saxatile, E. exile* and *E. blennioides* release between 3 and 15 and sometimes more. Eggs cannot be stripped from *E. nigrum* or *E. flabellare* without injury to the fish.

Correlated with this is a decrease in the number of males with which one female spawns in one spawning season and an increase in the contact time between male and female, a tendency toward monogamy. Thus there is a gradual decrease in the number of clutches laid. Again only the general trend can be outlined because detailed data are lacking. Observations of *P. caprodes* (lake and stream) and *H. maculatus* indicate that the female spawns once with a male and then shifts position so that usually another male is involved. Males of *E. caeruleum* and *E. spectabile* (presumably also *E. saxatile*) often spawn two or more times with one female, as do the other species with stationary territories. Females of *E. nigrum* lay from 30 to 200 eggs about six times with up to six males which is similar to the following two species. Raney & Lachner (1939) stated that *E. maculatum* lays 47-76 eggs two to four times with one to four males, whereas Lake (1936) found that a female of *E. flabellare* spawned five times, with a maximum of five males, laying an average of 33 singly deposited eggs. Each batch of eggs is laid with one male so that the pair remain together in the nest a longer period of time than is consumed in the brief contact made between the two sexes of the gravel spawners. It is not known how *E. (Ulocentra)* spp. fit into this framework, although on the basis of casual observation they appear to be intermediate.

In the laboratory, *E. blennioides* laid up to 100 eggs within a day or two and another batch was deposited 6-8 days later. The remainder of the eggs were absorbed. In the field, however, females of this species contained ripe eggs throughout the breeding season. This indicates that under laboratory conditions the large eggs are ripened and laid at a faster rate than in nature. This may be due to the higher temperatures and to the continual attendance of a courting male, who gives the female no opportunity to escape temporarily. This fact may explain why Fahy (1954) reported large clutches spaced by several days for *E. blennioides*. In nature the females of *E. blennioides* deposit eggs at a much slower rate, and the smaller eggs ripen gradually and variably as the mature eggs are laid. This seems to be true for most of the other darters except *E. nigrum, E. maculatum* and *E. flabellare,* which exhibit the most complex behavior. In the middle of the reproductive season, these specialized species may at times have no ovulated eggs, but they contain enlarged nearly mature eggs which constitute the next clutch. Before the previous clutch was laid, these were smaller.

Egg-laying by isolated females was observed in the laboratory in the following species: *E. caeruleum, E. spectabile, E. blennioides, E. exile, E. (Ulocentra)* spp., *E. nigrum* and *E. flabellare.* The other species probably can do this also but they were not observed a sufficient time in the laboratory. It presumably represents a reaction to the pressure of enlarging and ripening eggs in the ovaries, but after a small percentage of the total are laid, the reminder are absorbed.

EGGS AND THEIR CARE

The care of eggs by the darters varies from complete absence to a highly evolved type. The species which have no territory or only a moving territory bury their eggs in the gravel and this protects them from predation to a greater extent than if they were scattered on top of the substrate. This protection probably accounts for the fact that the largest number of eggs laid by any darter in a single season is about 3000 *(P. caprodes).* This is much lower than the number produced by many other fishes. Ellis & Roe (1917) recorded predation by suckers on *P. caprodes* eggs, and *Percina* eats their own poorly buried eggs. For this reason *Percina* must lay more eggs than *E. caeruleum* and *E. spectabile,* which also bury their eggs but do not ordinarily eat them. The dominant male of *E. caeruleum* and *E.*

spectabile in aquaria did not prevent other males and females of their own species from eating the eggs but only guarded the area around a female. In the field, females do not stay where the eggs are laid and sham battles between males eliminate most opportunities to eat the eggs. There is no direct care given to the eggs by *E. caeruleum* (Reeves 1907). *Etheostoma exile, E. blennioides, E. microperca, E. (Ulocentra)* spp., and *H. copelandi,* all with stationary territories, give indirect protection to their eggs against members of their own species solely by preventing their entrance into the guarded area. Only in the last species are the eggs buried in the gravel. Tendencies were noted earlier toward interspecific protection by *E. blennioides and E. (Ulocentra)* spp.

Etheostoma nigrum and *E. flabellare* care for the eggs directly. The male of the first species accomplishes this by four methods. He rubs the eggs with the pelvic and anal fins in an upside-down position. Also, he rubs them with his dorsals in an upright position or sends a current of water over them with his pectoral fins. Defense of the territory is maintained against most if not all possible egg predators. Eggs attacked by fungus are also eaten by the male. The male of *E. flabellare* rubs the eggs with both dorsal fins and sends a current of water over them with his pectoral fins. In both species, if the male is removed soon after the eggs are laid, the eggs become covered with fungus (Lake 1936, for *E. flabellare*). Indirect aid is given in that both darters attack all fish that are not too large which enter their territories. The eggs of both species are accessible and in a small mass so that in order to insure successful hatching they must be cared for and guarded. Since many of the other darters bury the eggs, added care is neither possible nor needed.

A partial correlation exists between increased care of eggs and a decrease in the total number of eggs laid. The total number of eggs laid by different age groups in one season is given for the various species in Table 4. In a few cases corrections are given on previous studies because the counts presumably did not represent the full complement laid in one season. The largest number is laid by *P. caprodes,* the species which gives the least protection to its eggs, and the fewest are laid by *E. nigrum, E. maculatum* and *E. flabellare,* all of which manifest a considerable amount of egg care. The comparisons are based on egg counts of equal age groups and the age distribution of mature adults. Within a species, egg number increases with the size and age of individuals. *Etheostoma nigrum* lays more eggs than is expected from the intricate care given the eggs (Table 2). Since the nest opening is usually larger and more accessible than it is in *E. flabellare,* the nest of *E. nigrum* may be more vulnerable to predation. Hankinson (1908) mentioned that *Pimephales notatus* frequently eats the eggs of *E. nigrum.* Although it appears that this species lays as many eggs as *E. (Ulocentra)* sp. and several other species (Tables 2 and 4), there are possibly more three-year-old and more mature yearling females in the populations of the latter species. This would result in a higher total egg production than that of *E. nigrum.* In fact there are a large number of three and four-year-old females in the populations of *P. caprodes, H. maculatus, E. caeruleum, E. spectabile* and *E. blennioides* when compared with some other darters. All yearling females of *E. microperca* were mature. Fahy's (1954) statement that the larger species produce a greater number of eggs is not borne out when the egg counts given by Petravicz (1936) for *E. microperca* are corrected. The latter author probably counted only ovulated eggs.

The total complement of eggs (all the eggs with yolk) normally is laid in one season. Fahy (1954) adequately demonstrated this for *E. blennioides,* as did Lake (1936) for *E. flabellare.* My data on these and most of the other species confirm their findings. By counting the eggs in the nest and in the ovary, Raney & Lachner (1939) also showed this to be true for *E. maculatum. Percina caprodes, E. caeruleum, E. spectabile, E. exile, E. microperca, H. copelandi* and *E. nigrum* lay their total complement of eggs, and it is presumed that the other species agree in this respect. The evidence which supports this contention is: specimens at the end of the breeding season have none of the eggs formed in the center of the ovary; ovaries dissected in the middle of the spawning season contain about one half of the total complement, and the previously smaller eggs are variously enlarged; females are found with ripe eggs throughout the spawning season; nest counts essentially agree with the numbers in preserved ovaries; and finally, Fahy (1954) was able to obtain deposition of all the eggs of *E. blennioides* in the laboratory.

Spent ovaries are made up of a mass of very small transparent egg-shaped bodies in the flattened wall of the ovary which are either oil globules or primordial eggs. Eggs that were counted were all opaque and larger and apparently represent all the oocytes in the ovary. As Fahy (1954) has shown for *E. blennioides* by histological sectioning the counts represent all the eggs with yolk. Apparently all that remains in the ovary are oogonia which soon after the reproductive season start differentiating into oocytes. The above results were all determined by use of a dissecting microscope. To verify these conclusions a histological study of the ovarian cycle in all species is necessary. In a few individuals some enlarged eggs were found in the process of being absorbed at the end of the spawning season, possibly because of variation in climatic factors. In ten or more specimens of each species, the counts of such eggs are as follows: *E. caeruleum,* 100, 200-500, and 200-500; *E. spectabile,* 50; *E. nigrum,* 200-300 (2 years old); *E. flabellare* 5 and 100. The other specimens had no eggs in the ovary. The spawning seasons are about 4-9 weeks in duration depending on the species of darter. All darters brought into the laboratory laid up to a hundred or more eggs in 1-5 days, and then the remaining, slightly enlarged ones were absorbed. Thus, laboratory evidence is

TABLE 4. Data on eggs of thirteen species of darters (*Percina, Hadropterus, Etheostoma*).

Species	St. L. in mm.	Age[a]	Total Number Eggs in Prespawners[b]	Av. Diam. in mm., Ripe (No. Meas.)	Hatching Time in Days	Temp. °C.	Source
P. caprodes	54.7 62.8-65.0 79.2-84.3	1 (1) 2 (3) 3 (2)	1060 ±2000 2712-3085	1.31 (10)			Author
H. maculatus	51.7 53.0	2 (1) 2 (1)	+1000 1758	2.0; 1.0 (10)	+6		Petravicz (1938) and Author
E. caeruleum	33.7 40.8-43.4 47.6-49.7	1 (1) 2 (4) 3 (2)	508 + 880 (734-1008) +1222-1462	1.56 (5) 1.78 (5)	10-11.5	17-18.5	Author
E. spectabile	29.7-33.0 36.1-41.8 44.7-45.6	1 (4) 2 (4) 3 (2)	717 (430- 896) 1254 (938-1480) 1758-2070	1.24 (5)	9.5-10	16.5-18.5	Author
E. saxatile	about same[c]			1.7 (5)	9-10	17-20	Author
E. exile	34.0-37.4 41.3-42.5 46.5-46.7	1 (4) 2 (4) 3 (2)	723 (550- 962) 1619 (1404-1798) 1912-2048	1.1 (9)	18.26	13.16	Jaffa (1917) and Author
E. blennioides	41.5-43.0 51.0-55.0 60.0-66.0 72.5	1 (3) 2 (3) 3 (3) 4 (1)	466 (404- 510) 784 (773- 799) 1500 (1462-1566) 1832	1.85 (5)	18-20	13-15	Fahy (1954) and Author
E. microperca	22.5-26.2 27.6-30.0	1 (3) 2 (7)	594 (435- 751) 858 (650-1102)	1.00 (10) 0.07	6.0-6.2	18-20	Petravicz (1936) and Author
H. copelandi	34.0-35.8	1 (3)	390 (357- 415)	1.4 (4)[d]			Author
E. (*Ulocentra*) sp. Barren R.	24.5-34.8 36.4-40.5 45.5-47.0	1 (5) 2 (3) 3 (2)	364 (181- 508) 798 (582-1194) 1222-1522	1.5 (5)	11-12	16-17	Author
E. nigrum	34.0-37.2 42.2-45.9	1 (4) 2 (4)	610 (436- 790) 1043 (750-1248)	1.46 (5)	7-8 5.5-6.5	22-24 22-24	Author
E. maculatum	40-47 50-51	2 (10) 3 (4)	242 (113- 357) 408 (402- 413)	2.0[d]			Raney & Lachner (1939) & Raney (pers. comm.)
E. flabellare	33 49 33-49	1 (1) 2 (2) 1-2 (23)	128 422-467 226 (128- 422)	2.3 (166) 2.22 (5)	30-35 21 14-16	17-20 av. 21-22 av. 23.5	Lake (1936) & Author

[a]numbers in parentheses denote number of specimens in which the eggs were counted for that age group.
[b]average, followed by range in parentheses; includes all eggs to be laid in one season.
[c]examination of females collected in the middle of the spawning season indicated the total number of eggs laid was similar to *E. spectabile*.
[d]preserved eggs; all others were fresh.

usually a poor criterion for determining the total number of eggs laid or the duration of the spawning season. This deviation may be due to insufficient food and other unknown biological factors. In the field, all the females are ripe for a period of 3-7 weeks (at least 3 weeks for *E. nigrum* and *E. flabellare*). Unripe or spent individuals can be found only at the start and the end of the reproductive period.

The eggs of all the darters are demersal and adhesive. When first laid the eggs are usually irregularly shaped, but after water hardening, they become essentially spherical as is common with teleost eggs. Winn (1953) described them as irregular in *H. copelandi* but used only freshly stripped eggs. Eggs laid against plants or rocks become flattened at the point of attachment, and small sand particles adhere to those buried in gravel.

Percina caprodes and *H. maculatus* have colorless transparent eggs usually with one colorless oil globule. The eggs of all the other species each contain one yellow or orange oil globule, and in some species the whole egg appears tinged with yellow. Some eggs of *E. microperca* seem to have several colorless oil droplets, whereas others are tinged with yellow. Egg size varies very little with the size of the adult and the number of eggs in the ovary. There appears to be a slight trend toward larger eggs in the complex spawners (Table 4).

In the two sampled populations of *P. caprodes* and several populations of *H. maculatus*, only rarely was a yearling fish found to be mature. Except for

these species, all but a few slow-growing individuals of the other darters mature in their first year. A few retarded specimens of *E. blennioides* were found, and Raney & Lachner (1943) reported the same situation for *E. nigrum*. Many individuals of *E. maculatum* and *E. blennioides* mature in one year, contrary to published evidence by Raney & Lachner (1939) and Lachner, Westlake & Handwerk (1950) who stated that they mature in the second year. Ovulated eggs were found in the ovaries of several yearling *E. maculatum*. The same was true for *E. blennioides* and most yearlings readily spawned in the laboratory.

Hatching time and temperature are given for some species in Table 4. From the data it is obvious that lower temperatures considerably delay the rate of development. Those eggs laid early in the breeding season take much longer to hatch than the ones laid later. This concentrates the hatching of young into a brief period which, if predation operates, may effectively reduce the percentage loss of the population (Darling 1938). The temperatures are too variable to demonstrate adequately if there are any differences between the species in time of development.

STIMULATION AND SYNCHRONIZATION OF BEHAVIOR

Various components of the environment and of the behavior of darters, such as fights, colors, movements, positions, the social organization, the presence of eggs and other elements, stimulate and synchronize the sexual partners in order to insure the simultaneous release of sperm and eggs in juxtaposition. Tinbergen (1951) summarized the possible stimulatory and synchronous effects of the various aspects of reproductive behavior. He divided synchronization of reproductive behavior into three stages: a gross synchronization brought about by the external rhythm, a more refined synchronization by "social releasers," and finally a precise timing by other "social releasers." Many aspects of behavior, such as the male following a female or fighting between males, apparently help to maintain the males in an intense reproductive state. The European school of behaviorists call these reactions "social releasers," but exactly how these are mediated internally is still questionable, and for this and other reasons the term is not used here (see Kennedy 1954 and Lehrman 1953). The older word, stimulation, is used in place of the above term.

Evidence was accumulated to demonstrate that fighting and other activities stimulated the reproductive behavior of males. In a few instances, with *E. blennioides*, *E. caeruleum* and *E. spectabile* several males and females were sexually inactive in an aquarium; the previously dominant male was neither aggressive nor chasing females. Upon the introduction of a mirror he attacked his image, attacked the other males, followed a female and spawned with her. An extra male is not absolutely essential for spawning, as is shown in the single-male experiments with *E. blennioides*, but one extra male is necessary for territorial expression. The males in the schools of *P. caprodes* may need contact with each other to maintain a sexually active state. Welty (1934) showed that individual behavior stimulated feeding activities of the group. It is known that certain school spawners used by aquarists are more successfully bred in large groups than in pairs. This may account for the lack of spawning by *P. caprodes* in aquaria. Darling (1938) suggested that the display and other activities of sea-bird colonies stimulate reproductive activity, and the schooling behavior of *P. caprodes* is similarly effective.

Both *E. nigrum* and *E. flabellare* establish only weak transitory territories, apparently stimulated by fighting and the nest site, until a female arrives and lays eggs, at which time defensive activities are increased. Even a non-territorial or sexually inactive male will begin to defend an area if a ripe female is added to the tank. The presence of a female under a rock excites the male to move rapidly around in circles in both the normal and upside-down position. These general effects were also observed in other species. In several instances where a small male of *E. nigrum* had set up a transitøry territory under a rock, another rock with eggs of this species was put in its place. The male was then stimulated to rapid activity in caring for the eggs and to a strong defense of the territory, even against much larger males. Therefore the eggs must have provided a certain stimulation. Other elements of behavior of a stimulatory nature are females swimming around males, males nudging females, and vibrations. The movements of females from pools to riffles and back again may help to stimulate reproductive activity, and many unsucessful excursions are made during the spawning season. Thus it would seem that many aspects of reproductive behavior maintain a male in an intense reproductive state so that egg-laying and fertilization are synchronous.

In many freshwater fishes there are two types of general population structures to insure contact between males and females for reproduction (Noble 1938). One is called the social school type, and the other the territorial type. Allen (1934) and Baerends & Baerends-van Roon (1950) used the term synchronization to mean the mechanisms that cause two animals of the same species but of different sex to be so adjusted that they are ready to mate at the same time. They restricted the term to the behavior between a pair, but it is here extended to include the population structure. It appears that this structure, which is limited to the few types to be discussed, is the first step in a series of adjustments that mediate the simultaneous readiness of a sexual pair to mate.

In fishes the social method involves the fish school or less compact aggregations. A migration usually occurs, at least in the north temperate zone, from the deeper water of a lake upstream, from a pool or riffle upstream to other pools, or from the ocean to inland waters. The males usually migrate before the females. In some species there is no migration, but a restricted area is maintained throughout the year (Gerking 1953). Since northern winter temperatures usually cause a period of inactivity, very few schools or territories are maintained throughout

the year. In the south temperate region, where winter temperatures are milder, the schooling or territorial society may remain intact throughout the year. Near the beginning of the reproductive season, schools are formed over the substrate in the general area where the eggs are to be deposited. The males predominate in these milling masses and the females maintain contact with them on the periphery of the group. When ready to spawn, the females move into a school of males and out again, followed by several males, to an appropriate egg-laying site, or they may simply move out from the mass of spawning fish. Two or more males in the mounted or clasped position is usual for oviparous fish which spawn in schools. There are numerous examples of this type of reproductive synchronization, particularly in the Cyprinidae. Some of the species which utilize this method are as follows: *Chrosomus erythrogaster* (Smith 1908), *Mylocheilus caurinum* (Schultz 1935), *Notropis spilopterus* (Hankinson 1930), and several catostomids (Reighard 1920). *Percina caprodes* is the only darter known to spawn in schools.

A second type of reproductive school in fishes combines both males and females within its structure. Here, the fish are free from the restrictions of the substrate for reproductive activities because they are viviparous. The live-bearers, *Lebistes reticulatus* (Noble 1938) and *Gambusia affinis* (personal observation), are good examples.

In most cases the formation of a fish school seems to be activated by a strong social attraction rather than by mere chance aggregation. If the fish gather over the breeding grounds because they react to a specific part of the physical environment, then the situation presents a different type of aggregation which does not involve a social reaction. If the males require contact with each other in order to form congregations over the breeding grounds, this formation may be a very primitive, loosely constructed type of school. *Stizostedion vitreum* may be an example of this type, and it seems unlikely at the moment that the term school should be applied to its population structure over the spawning grounds. The males of *Stizostedion vitreum* precede the females to the spawning grounds and several males simultaneously attempt to spawn with a female; the latter characteristic is typical for only the school spawners.

The second type of mechanism to insure contact between males and females, the territorial population structure, involves pugnacious behavior which serves as a spacing device. This type may also depend on social behavior, since the males may need contact with each other as in the school. For instance aggregations of sunfish nests may involve social behavior (Baerends & Baerends-van Roon 1950), although Breder (1940) suggested from experiments that such aggregations are determined by a reaction only to suitable nesting areas. In this case no social behavior would be involved. It seems more likely that a non-social aggregation might occur with pugnacious behavior because as the territory becomes more definite the reactions to the physical environment become more specific. As was true with the social structure, the territorial type usually involves a migration from the deeper waters of a lake, pool or ocean to a shore, riffle or pool. Gerking (1953) pointed out that such a migration may be absent in a few species of centrarchids in streams. The males migrate earlier to these areas where each maintains a certain space. The females then swim into these groups of males and usually spawn with only one male at a time. In species that exhibit a primitive pugnaciousness, however, one still sees attempts by more than one male to spawn with a female, such as in the yearling male behavior of *E. caeruleum* and *E. spectabile* (Winn 1958). All the darters studied here except lake populations of *Percina caprodes* fit the territorial type.

The social aggregational type of population structure in the reproductive season, accompanied by deposition of a large number of eggs, appears to be the basic generalized behavior in other fishes as well as in darters. Certain specializations may evolve within the loose aggregations such as the development of a highly evolved fish school or, as in the darters, pugnacious behavior is developed with a consequent new type of population structure. The intimate association of darters with the substrate may have strongly influenced the evolution of the territorial society.

A final series of reactions involves the responses between male and female once the female is in the school or territory. These are the "following," the "mounting" and the "quivering" responses, which complete the final synchronization of the spawning act. As described earlier the three sets of reactions are more complex in *E. nigrum* and *E. flabellare.* Evidence was accumulated that indicated temperature brought the darters into breeding condition. After this gross synchronization by the environment, migrations start, frequently a new population structure is formed, and a final series of reactions between males and females takes place which leads to the final fertilization of the egg.

SEXUAL SELECTION AND EVOLUTION OF BEHAVIOR

With our present background of information on the biology of fourteen species of darters we can now discuss sexual selection briefly and the evolution of behavior in considerable detail. Evolutionary trends based on behavior alone can then be compared to the results obtained by morphological studies.

Passive and possibly active sexual selection may occur in the darters. Reeves (1907) decided that the larger, more brightly colored males of *E. caeruleum* were selected by the females more often than the smaller less vividly colored males. Noble & Curtis (1939) and Noble (1938) presented evidence to show that the brighter (and possibly more active) male jewel fish is preferred by the female. They indicated that sexual selection can operate only if the females move through areas occupied by numerous males, so that a choice can be made. All the populations of

darters studied herein fulfill this requirement. That the larger males always locate in the center and deeper parts of the riffle first indicates that most of the females will mate with them, since the females tend to move through the center of the riffle. Whether they choose among these larger males remains to be ascertained, but which territory a female enters seems to be a matter of chance. Where there is a moving territory, a larger male will usually chase a smaller male away.

There is also a certain amount of structural isolation between age groups. Three-year-old males of *E. caeruleum* did not readily mate with yearling females, apparently because the size differences made it mechanically difficult. Yearling males and two-year-old males mated with yearling females. Yearling males spawned less easily with three-year-old females. Fahy (1954) showed that yearling males of *E. blennioides* which mated with an older female became spent before all the eggs were laid, whereas older males did not. In my studies, three-year-old males of *E. blennioides* readily spawned with most yearling females.

Some of the possible factors which are believed to control the distribution of darter populations and some of the structural factors that operate in sexual selection have been discussed. As shown in the previous sections it is apparent that many elements of behavior and morphology have changed as the darters evolved from the simple to complex types of reproductive behavior (Tables 2, 3 and 4).

It is assumed that some of the changes of behavior in the evolution of darters have survival and selective values. We know that some male darters protect only the eggs in their territories and will readily eat those defended by a male of the same species. Only a few darters defend their eggs against all species of a comparable size. However, we cannot conclude that primitive pugnaciousness developed for this reason, because in its initial stages territorial behavior centers only around the female, and the males dash only at male intruders of their own species. Here, early in the evolution of the darters, the territory may function to provide some sort of undisturbed pairing whereas finally, with the placing of eggs in situations vulnerable to predation, it was necessary to supply both interspecific as well as intraspecific protection. Various intermediate stages of defense were discussed in the section on territoriality. Thus through evolution there appears to have been a shift in the selective value of the territorial society. Because of their small size, *E. nigrum* and *E. flabellare* cannot defend the nest against relatively large fish, like some minnows; consequently there has been a selective advantage for these species to lay their eggs on the underside of rocks. Here the larger predatory fish cannot get at the eggs easily. Inability to defend against larger fish may have prevented *E. caeruleum*, *E. spectabile* and *E. saxatile* from developing further toward the gravel-nest building habit. The fluviatile minnows which exhibit this behavior are usually larger.

Many of the factors associated with behavioral responses to eggs may be merely physiological necessities and consequences. Fewer eggs may be laid because more energy is channelled into courtship activities, territorial defense and egg care. An objection to this explanation is that most of this added behavior is carried on only by the male; it has not been proven that the female utilizes more energy in these activities, and observation on the darters makes this seem unlikely. Svärdson (1949) realized that it would be selective for a fish to lay more eggs, but counteracted this by showing that there is a selection for larger eggs and larger larvae—thus fewer eggs. This presumably would give the young a better start in life. If this were so, there might also be a selection toward larger fish, which is not true, especially in darters. However, in their evolution, the darters show a positive increase in egg size, which supports Svärdson's idea.

Although in some instances the function of the territory is quite understandable, the selective processes are not so easily comprehended. They may be more intelligible on a population basis when the relationships of the many aspects of behavior that evolve with changes in territorial behavior are clearly related to population phenomena.

Species from different morphological lines of evolution within the subfamily Etheostomatinae were studied in relation to behavior. The genera *Ammocrypta* and *Crystallaria*, and several subgenera, were not included. The behavioral and associated trends are shown in Tables 2, 3 and 4, in which the species are arranged as nearly as possible in order of increasing complexity. Table 2 attempts to summarize much of the previous data in an abbreviated form. Each aspect of behavior has been discussed in detail under the appropriate section. The morphological relationships are shown in an evolutionary tree (Fig. 7). From the study of this representative group of species, it is possible to describe a behavioral prototype and many of the evolutionary consequences.

The primitive and less complex type of reproductive behavior in the darters is the non-territorial gravel type of spawning. Other primitive characteristics are as follows: the eggs are scattered in moderate numbers over a wide area of gravel (at least 10-20 eggs at a time); a large total number of colorless eggs are laid; females spawn many times with many males; neither a territory nor parental care is manifested; a social type of reproductive behavior occurs; the male mounts the female when she stops; sexual dimorphism and sex recognition are weakly developed; the sexes are of equal size or the male is smaller (Raney & Lachner 1943); and the reproductive habitat is in large streams and along lake shores. The species that exhibit these types of behavior are relatively large, and mature in their second or third year.

An evolutionary sequence may be hypothesized as

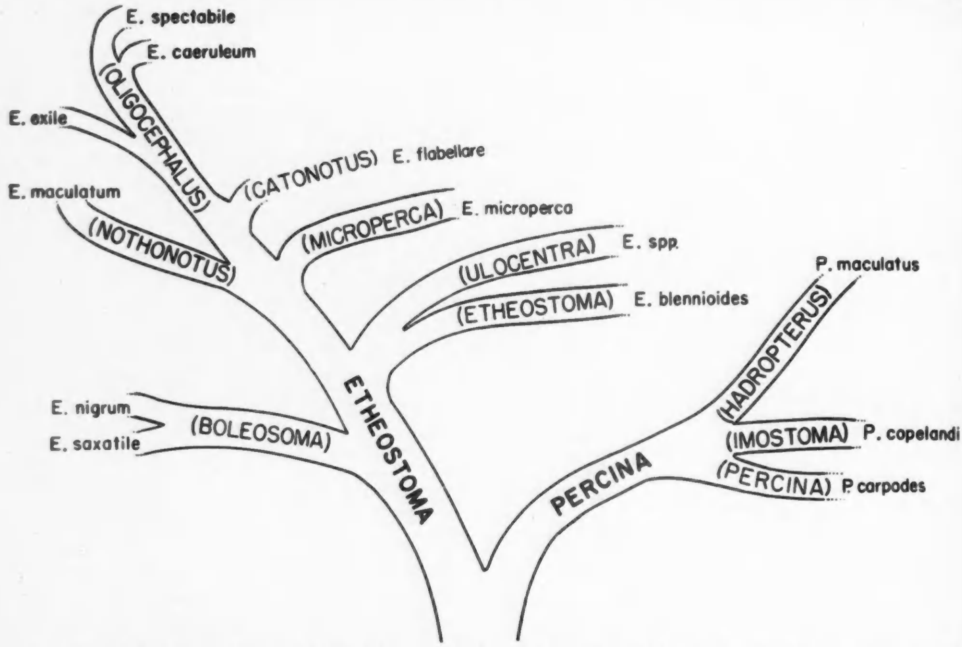

FIG. 7. Preliminary scheme of the phylogeny of the darters whose behavior is considered here, based on morphological characters (by Reeve M. Bailey, unpublished material). The genera are in bold print and the subgenera (former genera) are in parentheses. The genus *Hadropterus* is now considered by Bailey to be a synonym of *Percina*, a change which is not followed in the text.

follows. Early percids with a large air bladder first swam freely in the water; then, the fish spent more time on or near the bottom with the concomitant loss of the air bladder in many species. As soon as a part of their life history included only movements on or near the substrate, three distinct food stages appeared; a surface entomostracan food habit, a midge and other small insect larvae food stage, and finally a more varied larger insect diet (Turner 1921). The population of *Percina caprodes* in Douglas Lake exhibits most of the primitive traits described above.

Very early in evolution a primitive type of territory, expressed as simple pugnaciousness between males, was superimposed upon the generalized pattern. Territory in its earliest form consisted of slight dashes by one male toward an intruding male while the former followed a female. The intruder left as a consequence of this movement toward it. Ritualized fights for space and females did not occur. Spawning took place over a wide area, although this was smaller than the escape and food ranges. Stream populations of *Percina caprodes* and *Hadropterus maculatus* fit this situation. The elements of space, number of eggs laid, sex recognition, etc., evolved concomitantly to some extent.

As the darters evolved, many changes took place which may have involved some genetically linked characteristics or correlated physiological phenomena not necessarily of adaptive value. The choice of habitat changed drastically; many species moved into riffles and into moderate sized streams, after which there were several secondary invasions of still water. Reactions to particular aspects of the environment became more specific. Other changes of behavioral and associated elements appeared (Tables 2, 3 and 4): the reproductive period started later in the spring in slower current; sex recognition became more precise; a winter territory was added; territorial protection was no longer strictly intraspecific, but became also interspecific; the food and escape ranges coalesced with the reproductive territory, and this decreased in size as did the area in which the eggs were laid; a tendency toward monogamy dominated; and parental care increased. Other elements changed as follows: sexual maturity was attained in one year; within limits, the body size decreased; the size of eggs increased; the total number of eggs decreased; the number of eggs released at one time diminished to one; and the eggs became yellow.

The "following" reaction remained unchanged until reproduction became very specialized, as in *E. nigrum* and *E. flabellare*, but the stimulus which elicited the "mounting" reaction by the male changed considerably. In the earliest stages the male mounted the female when she stopped in a horizontal position. In two species, *E. caeruleum* and *E. spectabile*, the female exhibited a gravel-burying stimulus. In the advanced forms, prods by the male and upside-down movements apparently functioned similarly. It does not seem likely that the more complex forms went

through a stage in which the female exhibited a gravel-burying reaction. In most species the final fertilization was initiated by the simple tactile response of male-on-female, but again in *E. nigrum* and *E. flabellare* male prodding and upside-down movements under the rocks served this function. During evolution, the spawning position of the pair gradually changed from a normal horizontal position to an upside-down position. The mounted position of the male on the female remained the same until the spawning position reached a strongly obtuse angle, when the position of the two sexes was side by side.

Certain characteristics showed little or no modification as evolution proceeded. The adhesive and demersal egg retained the same form. The bottom swimming habits of the darters, particularly their use of the pectoral fins, seem to be characteristic of the group. Another conservative character is their habit of feeding on the bottom, which results in the utilization of chironomids as a primary food (Turner 1921, and personal observations). Generally speaking, darters are of small size and, except for lake populations of *Percina caprodes*, exhibit territorial behavior.

In an advanced form such as *E. nigrum*, one can trace some of the major steps in behavior involved in a transition from the primitive type to its present behavioral complexity. From the prototype with non-territorial, schooling behavior in slow water and spawning in a horizontal position, evolution proceeded to a gravel spawner which was slightly pugnacious and moved freely over the gravel in moderately fast water. This stage is typified to various degrees by *H. maculatus*, *E. caeruleum*, *E. spectabile* and *E. saxatile*. At this point, or when the behavior was more complex, there developed a tendency to spawn later in the spring and thus in a slower current. The male soon limited his pugnaciousness to a particular spot in the gravel associated with a large rock inside the territorial boundaries, and the eggs were still scattered over the gravel. The behavior of *H. copelandi* fits this stage. Soon, however, the eggs were scattered one by one over a large rock in a vertical or nearly vertical position. The two forms of *Etheostoma* (Green River and Barren River), both in the subgenus *Ulocentra*, exhibit this intermediate type of behavior. Then, slowly, the adults tended to spawn more and more off the vertical towards an upside-down position. Finally, as exemplified by *E. nigrum* today, spawning took place only in this position. A strong territoriality was present and the eggs were laid in contact with each other. Througout this evolutionary history the darters at any given time and place probably exhibited different percentages of the various types of behavior. These changes, culminating in *E. nigrum*, probably involved a sequence of behavioral types as is typified by *P. caprodes* (lake), *H. maculatus* or *P. caprodes* (stream), by *E. caeruleum* or *E. spectabile*, and by *H. copelandi* and *E. (Ulocentra)* species (Tables 2, 3 and 4).

The one major type of reproductive behavior found in stream fishes of North America which is not represented in the darters is the construction of a gravel nest. Reeves (1907) thought that the behavior of *E. caeruleum* represents a stage in the evolution of the nest-building habit. Its future development would depend on whether the species could defend their eggs against larger predators.

The plant spawners represent different lines of development. The habitat of *E. microperca* illustrates a secondary invasion of quiet water. This species presumably went through the early stages described for *E. nigrum*, and its territory finally became fixed in an area with plants. The behavior of *E. exile* may represent an intermediate stage in this development, with the tendency to lay eggs on roots and fibrous clumps of earth in areas where plants are common. From this stage it is an easy step to the use of plants for egg deposition. The above plant spawners also appear to be exceptional in that the female is larger than the male. *Etheostoma blennioides*, on the other hand, has gone through much the same evolutionary stages as *E. nigrum*, with some exceptions. *Etheostoma blennioides* has moved up to spawn semi-vertically on large algal-covered rocks in fast water. Thus the eggs were soon, if not immediately, laid partially on the alga, with no intervening stage of egg laying on the side of the rock. This must have selective advantage over any other tendency. The large total number of eggs laid and the fact that several are laid in one vibration suggest a direct transition from gravel deposition to the placement of eggs on alga. Also, when *E. blennioides* abnormally spawns vertically against the side of a tank, the eggs do not adhere, which they might be expected to do if the species had gone through an intermediate evolutionary stage.

Up to this point we have traced in some detail the supposed evolutionary trends of behavior in darters. It is now necessary to discuss the basis of our conclusions. Why is it that evolution of behavior has not proceeded in the opposite direction from that discussed? The study of comparative behavior relies on the same principles that are used in comparative morphology. It is subject to the same degrees of accuracy and error in the interpretation of evolutionary sequences. The assumption is made that the comparison of the behavior of a group of related species, in this case the subfamily *Etheostomatinae*, may provide information of phylogenetic significance. Their behavior patterns should be homologous, have common trends and have common roots of origin. Therefore we can decide on evolutionary patterns based on behavior alone as we have done so far.

The exceptional and complex can often be considered to be derived from the common and less complex. The reproductive behavior of *E. flabellare*, *E. maculatum* and *E. nigrum* is complex and exceptional and thus we may infer that it was derived from common and less complex habits, as exhibited in gravel-spawning types. The primitive traits progressed through intermediate stages to the specialized

ones. Complexity in the darters also involves narrowly adaptive characters which restrict or limit the habits of species or group. These are usually specializations which are secondary or more recent in origin (Mayr, Linsley & Usinger 1953: 169). The modifications by *E. nigrum* and *E. flabellare* of the simple "following," "mounting" and "quivering" reactions are considered to be more complex, as is the addition of care of the eggs. A fish which lays a fewer total number of eggs is regarded as a specialization in this group. A narrowly adaptive, specialized type of behavior is exhibited by *E. flabellare* which lays its eggs under a rock just the height of the fish's body off the bottom. Gravel-burying and the upside-down position are considered to be specialized behavior and more narrowly adaptive.

Laboratory evidence derived from a study of *E. nigrum* and *E. flabellare* contributed to the conclusions with respect to the evolutionary steps as outlined. When the two species were placed in aquaria without the proper rocks, the females laid eggs vertically on the slate walls of the tank. There the eggs were immediately eaten. It is postulated that this manner of deposition is a reversion to an immediate ancestral type of egg-laying habit (James W. Atz independently presented this idea in a personal communication). In the absence of algae, *E. blennioides* laid eggs on the walls of the tank and these fell onto the gravel bottom. At other times they were laid directly on the gravel. The eggs were eaten immediately in both instances. *Etheostoma* spp. (Barren and Green R. forms) also laid eggs in the same manner when not given an appropriate rock on which to deposit them. The eggs of *E. microperca* were laid only on plants unless these were insufficient for the number of spawning pairs, in which event successful reproduction occurred on the roots, rubble or on the bottom gravel. *Etheostoma exile* deposited its eggs on fibrous clumps of earth or roots, but if only sand or gravel were present the eggs were successfully laid there. These latter two examples are considered true variations in reproduction, with the sand or gravel egg deposition as a trait on its way out. The substitute type of egg laying is contended to be the prior or directly ancestral type of reproduction.

The phylogeny as presented is also thought to be the simplest interpretation. If the reverse trend in the evolution of the darters is considered, one would have to postulate that the air bladder was first lost by certain darters and then evolved again. This type of explanation would have to be applied to behavioral characters.

Certain difficulties arise when we infer evolutionary trends because of the phenomena of convergence, parallelism, shuffling of generalized and specialized characters and the exceptional trend from the specialized to the less complex. The similar egg deposition sites of *E. flabellare, E. maculatum* and *E. nigrum* are examples of parallelism. But on close examination the resemblances in this behavior are seen to be superficial. These species show noteworthy differences in the spawning positions and in the care of eggs. *Etheostoma maculatum* lays a several-layered wedge-shaped mass of eggs, whereas the other two species lay a single-layered patch of eggs. The morphology of the three species clearly relates them to what have been called, until recently, three different genera. The use of organic debris and plants for egg deposition by many species is also a parallelism. However, there is no evidence to indicate that the procession of the prototype darter to the various descendants is not in the direction stated. Simpson (1945: 5) said, "Phylogeny cannot be observed. It is necessarily an inference from observations that bear on it, sometimes rather distantly, and that can usually be interpreted in more than one way."

The evolution of behavior of darters has been outlined on the basis of biology alone and the reasons upon which the direction of evolution was based were discussed. In general the major outline of evolution based on the behavioral studies agrees with the ideas expressed by the taxonomists based on morphology alone.

Most of the darters have lost the air bladder, with the exception of *Percina,* and many species of *Hadropterus* which have a small air bladder. For this and other morphological reasons, *Hadropterus* and *Percina* are considered to be primitive darters by taxonomists (Jordan 1929; Bailey 1951. See also Fig. 7, where Bailey has briefly outlined his ideas on evolution in darters based on morphology). Behavior studies support this conclusion, for it is precisely in these two groups that the least complex, and hence the most primitive type of behavior is found. An increase in complexity of behavior patterns seems to parallel morphological specializations. There are some species of *Hadropterus, copelandi* for example, which are more specialized morphologically, and in that particular species the behavior is also more complex. Thus as a group many of the species within *Percina* and *Hadropterus* now represent a large side branch in evolution but still retain many of the more primitive characters lost in the other groups of darters.

Etheostoma saxatile and *E. nigrum* are included in the subgenus *Boleosoma* on morphological grounds, although *E. saxatile* was at one time placed in the genus *Doration.* However, their behavior patterns differ distinctly. A southern member of the same subgenus, *Etheostoma chlorosomum,* lays its eggs on plants or debris (Clark Hubbs, personal communication). Such diversity of behavior in a single subgenus, which involves the use of such conspicuous elements of the fresh-water habitat as gravel, plants and large rocks, strengthens the view that the *Boleosoma* species-group was isolated early in the evolutionary history of darters and became independent of the other lines. This agrees with Bailey's idea based on morphology (Fig. 7.) However, the placement of *E. saxatile* in the *Boleosoma* group will have to be carefully reconsidered. The fact that *E. nigrum* and other species of the subgenus not dis-

cussed in this paper (unpublished material in progress) have complex breeding habits disagrees with the placement of the *Boleosoma* group as the closest living relatives to the basal stock of the large genus *Etheostoma*. This conflict can only be resolved when more information is available. The same diversification of behavior in *Boleosoma* seems to have occurred with at least one species in each of the subgenera *Oligocephalus, Catonotus* and *Ulocentra*. This supports the idea that each of these groups has been set off as a small side branch in evolution for a long enough time to evolve (Fig. 7). The evolution of darters is closely tied to the variability of the substrate, since they utilize many different components of the habitat for egg deposition. Rubble is used quite frequently in the north by such forms as *E. blennioides, E. (Ulocentra)* spp., *E. nigrum, E. maculatum* and *E. flabellare*. Along the Gulf Coast, where the rubble habitat is essentially absent, plants take the place of large rocks. *Etheostoma lepidum, E. grahami, E. fonticola, E. proeliare* and *E. chlorosomum* all lay their eggs on plants or plant debris in Texas (Clark Hubbs, personal communication). The first three species belong to the subgenus *Oligocephalus,* the fourth to the subgenus *Microperca,* and the last to the subgenus *Boleosoma.*

Variation in behavior correlates with variation in morphology. It appears that any divergence between behavior and morphology reflects only a lack of knowledge by the biologist. This comparison of the behavioral evolution of darters with the morphological evolution presents agreement on the general trends insofar as the morphologically primitive species are behaviorally primitive and the morphologically specialized are behavorially specialized. Apparent conflicts in several areas need to be reconsidered. Some of these questions should be answered as more information is accumulated on behavior and morphology of this group of fishes which have evolved a wide variety of habits within their territorial bottom-living societies.

SUMMARY

The reproductive behavior and ecology of 13 species of darters were studied comparatively both in the field and laboratory. The work was done in the Ann Arbor area, Michigan, and in Kentucky and Tennessee. Raney & Lachner (1939) studied the 14th species considered here.

The microhabitat for each species is discussed and it is shown that there are seasonal, age and sexual differences. Spatial and temporal isolation of the microhabitats among the darters and other fishes is so arranged that competition is negligible.

Most darters migrate to and from the spawning grounds. Other characteristics of the migrations are described. In the summer and fall certain rubble-riffle inhabitants move downstream, which is apparently caused by a decrease in the flow of water.

Periods of abnormally cold weather stop both migration and reproduction. Interspecific, intraspecific and yearly differences in the reproductive period are discussed. Those species which exhibit the most specialized and complex reproductive habits spawn later in the spring and have shorter breeding periods than do those with more generalized breeding habits. It is suggested that the slower current of the late spring is important to these complex spawners.

Various aspects of territorial behavior and activity ranges are discussed in detail. The areas utilized by the fish are divided into the territory (male), the reproductive range (female), the food range, and the escape range. Most activities cease at night. All the darters exhibit pugnacious behavior except lake populations of *Percina caprodes*. The area guarded is either around the moving female or around some conspicuous element of the habitat, such as a rock or plant. A trend toward interspecific defense of the territory and the development of a smaller territory is apparent. Some species have a non-reproductive territory. In a series of experiments on *Etheostoma blennioides,* it was shown that the presence of other males at the time of egg-laying is necessary for the expression of territorial behavior. The social and ecological situations are important for territorial expression. Fighting behavior, dominance relations, size of territories, and functional aspects are discussed.

Sexual dimorphism is exhibited by the shape and size of the fins, the kind and distribution of pigment, the body size and the structure of the urogenital papillae. Highly evolved territorial behavior is related to an increase in the size of the male over the female. The more striking fin modifications in the males are correlated with complex behavior and with the use of these structures either to clean the eggs or to maintain a certain spawning position. A preliminary system of sex recognition is postulated and some of the differences between species are discussed. Some features of sex recognition are as follows: in a few species males are not recognized, whereas, in other species males recognize each other by their bright hues; and males identify females by certain movements which differ for the various species. Males and females in the mounted position are tactually stimulated to vibrate, at which time the eggs are laid and fertilized. There is a close correlation between behavior and morphology especially between sex recognition, territoriality and sexual dimorphism.

In most species, very few activities can be designated as courtship. However, certain movements of the females toward males are considered as such. Reactions between the males and females, that lead to the spawning act, are divided into the "following," "mounting" and "quivering" reactions. The three species that exhibit the most complex behavior, *E. nigrum, E. maculatum* and *E. flabellare,* deviate from this pattern. During the spawning act the male is on the back of the female except in the above three species, which lay their eggs in an upside-down position. The various angles at which the different species spawn are described. There are a considerable

number of differences between species in the number of eggs laid at a time, the number of clutches laid and the number of males with which a female spawns.

Variation in the care of eggs by the males of the different species exhibits a trend from complete absence, to indirect care, and finally to fanning and cleaning the eggs. A partial correlation exists between increased care of eggs and a decrease in the number that are laid. Total egg counts are given for each species which are all laid in one season. The eggs of all species are adhesive and demersal. Most species mature in one year.

Contact between males, either in a school, a looser aggregation or in territoral defense, is considered important to the maintenance of an intense sexual state. The eggs and nest site are also stimulatory. The organization of the schooling and territorial societies is regarded as the first step in reproductive synchronization which is finally accomplished by the "following," "mounting" and "quivering" reactions.

Certain aspects of sexual selection are discussed. The selective value of the territory and associated behavior are considered. At first the selective value is probably intraspecific, but this changes when the defense is also against other species. Finally, a phylogeny of behavior for the darters is presented. The basis for such a phylogeny is discussed in detail. Those species regarded as the most primitive on morphological grounds are also the species which exhibit what is considered to be the most primitive behavior. Also, the darters with more specialized and narrowly adaptive behavior are generally considered the most recent in origin on morphological grounds.

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RESPONSES OF VENUS FLY TRAP (*DIONAEA MUSCIPULA*) TO FACTORS INVOLVED IN ITS ENDEMISM[1]

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INTRODUCTION

Probably the first mention of *Dionaea muscipula* was under the name of "Catch Fly Sensitive" by Governor Dobbs of Brunswick, North Carolina in letters to Peter Collinson of England in 1759 and 1760 (Harper 1942). In the letter of April 2, 1759 Dobbs said, "We have a kind of *Catch Fly Sensitive which closes upon anything that touches it.* It grows in this latitude 34 but not in 35°." It was John Bartram of Philadelphia (King's Botanist) who first sent specimens to Collinson in 1763 (Darlington 1849). These were passed on to Ellis and Solander, along with other North American plants for study. The excitement with which Collinson received Dionaea is expressed in a letter to Bartram dated May 10, 1763 in which he said. . . . "Think my dear John, with what amazement and delight I, with Doctor Solander, surveyed the quire of specimens. . . . But what surprises us most, is the *Tipitiwitchet*[3] Sensitive. It is quite a new species, a new genus. It was impossible to comprehend it from any description, which made me so very impatient to see it." Ellis recognized its affinity with Drosera, but since the material was dried he was unable to comprehend the sensitive mechanism until William Young brought living material to England in 1768. Then, in 1769 in a letter to Linnaeus, Ellis wrote the first botanical (Latin) description of Dionaea which he published in 1770 together with a colored plate (Fig. 1).

Dionaea, a monotypic genus within the family Droseraceae, is endemic to the central southeastern coastal plain of North America, and has, since its discovery, stimulated botanists and naturalists to much investigation, discussion, and speculation, particularly concerning the nature and action of the leaf. The important contributions to knowledge of Dionaea up till 1942 were thoroughly reviewed by Lloyd in his book on "Carnivorous Plants." Since then only a few papers on Venus fly trap have appeared.

The unique characteristics of Dionaea are widely known among botanists and have made it the subject of a great diversity of studies. Rather surprisingly it has been given no attention, in terms of endemism or senescence, by phytogeographers but this neglect may be related to the general lack of information on its ecological responses and requirements. No orderly study of Dionaea from this point of view has ever been attempted. Only perfunctory and incidental descriptions of its habitat and ecological characteristics are available. Thus it was with the hope of con-

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[3] "*Tipitiwitchet*" was the name by which Bartram and Collinson knew Dionaea until the time when Ellis named it.

FIG. 1. Ellis' illustration of ***Dionaea muscipula*** sent with his letter to Linnaeus in 1769. Made from a living specimen brought to England by William Young. The drawing is in error in that the internodes of the flowering rachis are too long and that the terminal flower always opens first, rather than the proximal laterals.

tributing to the understanding of the ecology of the species that the present study was initiated.

RANGE AND DISTRIBUTION OF DIONAEA

Since the discovery of *Dionaea muscipula* by Governor Dobbs its range has been somewhat ill-defined, with the general consensus being that it is limited to an area around Wilmington, North Carolina. This misconception was dispelled in 1928 when Coker published a map of its range, as accurately as known at that time, and discussed briefly the locations given by various collectors.

To supplement Coker's report, a list of all Dionaea specimens in 19 American herbaria was obtained together with whatever information, often extremely meager, that appeared on each label. Then an attempt was made to relocate as many as possible of the reported stations. In addition, much time was spent searching for unrecorded stations, especially during the flowering season when the plants are most easily noted. Personal contacts with botanists, naturalists and farmers provided much supplementary information and led to several new records.

The field and herbarium search indicated that the species is much more widely dispersed in some areas than expected and in others is more restricted. It soon became apparent that human activities and absence of fire are very important in restricting the occurrence of Dionaea.

As to reported range limits, the most northern station near Chocowinity in Beaufort County was probably very nearly relocated (Fig. 2), but even this station has since been demolished by the erection of a sawmill. It is likely that careful search in the vicinity, particularly during the flowering season, would turn up more plants, because there are numerous localities here which appear to be favorable for them.

The southern limit on the Santee River (Charleston County, S. C.), based on a report by General C. C. Pinckney, was unconfirmed at the time of Coker's paper, but a new location was found there in 1949 by Bell (University of North Carolina Herbarium). However, the herbarium label indicated that only 3 plants were seen at the site. Although our search in the area in 1956 failed to verify its continued presence, it is probable that a more extended exploration would confirm it, particularly as there are numerous apparently favorable habitats in the vicinity, fire seems to be fairly frequent, and agricultural development is at a minimum.

The western limit seems fairly well established in Moore County, but farming practices of that region have probably brought about its extinction as it could not be relocated though every effort was made to do so. It was relocated in the Fayetteville area, but the erection of a Ball Park on this site suggests its imminent disappearance from here as well.

The accompanying map (Fig. 2) gives the distribution of the plant as inferred from herbarium material, and confirmed by observations during the course of this work. The herbarium locations are marked by open circles, the relocated areas by double circles and the new stations by black circles. Specimens from all newly reported stations have been deposited in the Duke University Herbarium. The main difference between Coker's map and the one given here is in the general limits of the range. Coker does not show any location south of Georgeville, S. C. but gives a location in Wayne County, N. C. No evidence has been found in field work or from herbarium specimens to support this latter observation.

Apparently, as Coker and earlier writers believed, *Dionaea muscipula* is not doomed to extinction in North and South Carolina, but its range may be severely curtailed by human interference and land usage. In many undisturbed areas, particularly in Brunswick, New Hanover, Bladen, Onslow and Carteret Counties in North Carolina and in Horry County in South Carolina, great numbers of plants are present over wide stretches of land which are not likely to be used in development. The increasing use of controlled burning by foresters in these areas may contribute to its survival.

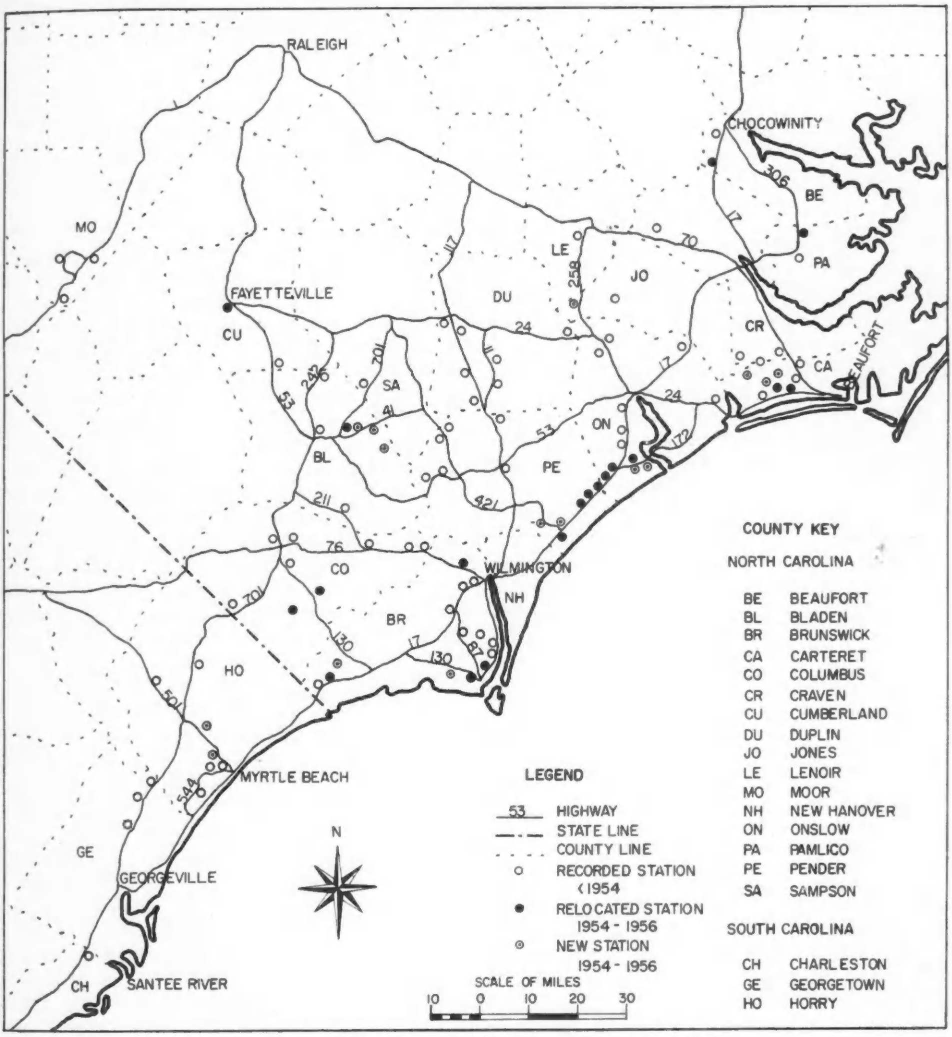

FIG. 2. Map of the distribution of *Dionaea muscipula.*

GEOLOGY OF THE DIONAEA TERRITORY

The coastal plain of the southeast was deposited during the late Mesozoic and Cenozoic on a horizontal or gently sloping basement in the Atlantic Ocean. The Pre-Pleistocene sediments are chiefly marine but the origin of later ones is controversial. As many as seven successively younger terraces have been recognized between the Fall Line at about 270 ft elevation and the coast, each presumably marking a marine inundation during an interglacial period. However, Flint (1940) considers only the four lowest of these terraces to be marine, designating the youngest as Suffolk and the next three combined as the Surrey. Richards (1950) considers only the Suffolk to be marine and all the others between it and the Fall Line as mainly alluvial in origin. These latter sediments are, in the main, not fossiliferous or contain only plant fossils (Dr. E. W. Berry, personal communication).

Most of the Dionaea habitats of the lower coastal plain are on the Suffolk and Surrey terraces where the chief sediments are sands. These sands make up the greater part of the derived soil. The Suffolk and the Surrey date from the Sangamon and Yarmouth interglacials (120,000 and 250,000 yrs ago). The age of the superficial sands in Moore County is questionable. The underlying Tuscaloosa formation is a sand of Upper Cretaceous age but the overlying sands, considered to be a relic of former shore lines and forming the sand hill region, are probably Pliocene or Pleistocene. Although the Pleistocene and more recent sediments are mainly sands, silts and

clays of alluvial origin, beach sand is also present, as well as peat accumulations in areas of high water table.

Any ideas on the geologic history of Dionaea, or even of its migration in relatively recent time, must be conjectural. Fossil pollen from bog studies might be helpful but none has been recognized. Nevertheless, the history of the development of the coastal plain invites speculation on the occurrence of Dionaea during this time.

During the Mesozoic and Cenozoic the present sandhills of Moore County presumably were dunes along ancient coastlines much like those along the present south Atlantic coast. If, at that time, there were climates similar to the present, there must also have been habitats like those now existing in the lower coastal plain, including sites where Dionaea could have grown. Such conditions and the occurrence of Dionaea were possible through Pliocene time. With the gradual exposure of the coastal plain during the Pleistocene, migration of Dionaea to the south and east could then have occurred, as suitable habitats became available, and could have continued until the present range was reached. Perhaps the range was once greater than it is today; perhaps the potential range has not yet been attained. The present climate and distribution of habitats suggest that a wider range might be possible but the evidence for a conclusion is inadequate.

FIELD OBSERVATIONS

General Description of Dionaea Habitats

It cannot be said with any certainty that Dionaea will be found wherever the conditions described below occur, but it can be stated with confidence that the macro-conditions within Dionaea locations are similar over a wide area.

Typically, Dionaea grows in semi-pocosin (or semi-savannah) areas or, where pocosins are limited, in zones around their edges. Thus, it is immediately established that the habitat is intermediate between the wet evergreen-shrub bogs, and the dry sandy regions of the surrounding longleaf pine—wire grass savannahs. Canby in 1868 said of its habitat: "It is somewhat singular that this little herb is only found in the vicinity of Wilmington in North Carolina, and the adjacent parts of South Carolina, where it is comparatively common in the damp rich soil bordering the bogs and swamps." Dean (1892) pointed out, using an area east of Wilmington as an example, that "the plant is not, as often supposed, a native of dry and sandy flats, nor like Drosera, common on moist mud flats, nor yet on the high brinks and plant covered banks of large stagnant pools. It appears to be less general in its actual place of occurrence than the common predatory plants that are well represented in this region." Thus, both workers recognized the ecotonal nature of the habitat, a fact often overlooked by collectors as most herbarium records merely list "savannah" or "bog."

There has been little comment on the nature of the soil. Ellis (1770) described it as "a light black mould intermixed with white sand, such as is usually found on our moorish heaths." Canby's conception of the soil as being "rich" was evidently based on the dark color; it is, in fact, very infertile as will be shown in a later section. No other observations have been recorded on this topic, except that Wells (1932) remarked that the soil "does not become excessively wet or dry."

Frost tolerance is not a trait usually associated with Dionaea, but this has been recognized from the time of its first discovery. Bartram, in a letter to Collinson dated May 1st, 1763, says: "I have one root of the *Tipitiwitchet*. It bears our winters [Philadelphia] —is strong this spring" (Darlington 1849). Canby also pointed out its hardiness and recently Mr. Henry Wright of Highlands, North Carolina, transplanted it to the mountains, where it has survived for several years and even produces flowers every summer. During 1956-57 unprotected plants survived frosts in Durham, N. C. down to 10° and 12°F without any ill effects and continued to grow, though slowly, through the whole winter. No mention of tolerances to hot weather exist except Ellis' comment on the climate of the original location: "swamps of North Carolina, near the confines of South Carolina about the latitude of 35° North, where the winters are short and the summers very hot."

Fire is common in all Dionaea areas, and as a result the ground vegetation is sparse, and the soil often has a "pepper and salt" appearance due to the incorporation of charred and decaying organic material into the white sand. Sometimes there is a shallow layer of peaty material above the inorganic soil. There are no species which are always in association with Dionaea but instead a mixture of savannah and bog types with wide moisture tolerances (e.g. Ilex, Zenobia, Lyonia, Polygala, Liatris, Aristida). Not all of these occur in every location and in different places the proportions vary. However, there are three other insectivorous genera (*Pinguicula*, *Sarracenia*, and *Drosera*) which nearly always occur with flytraps in varying abundance. The land where Dionaea grows is generally completely flat or with less than a 3% slope; where this slope is present, as is usual around a pocosin, populations have quite well defined boundaries: a dense shrub zone at the lower side marks one limit while the other is apparently determined by the summer depth of the water table. Over wide flat areas especially in several of the southeastern counties, Dionaea is distributed throughout large tracts of land which have not been disturbed. It rarely grows in depressions where water is likely to collect, but on the edges of such positions, a fact also noted by Dean (1892). Such hollows which have filled with Sphagnum, sometimes support Dionaea but these are not typical habitats. In the usual site the surface of the ground is generally damp, except that at the upper limit of a population zone it may become completely desiccated to a depth of several inches during the driest part of the year. The

sand in these positions may be almost snow white at the surface due to the lack of organic matter and pluvial action.

Dionaea may at times colonize disturbed areas if competitive growth is at a minimum. It is not uncommon on the right-of-ways of railroads, where vegetation is kept under control by constant cutting or burning. The best example of this type of colonization is along the Atlantic Coast Line Railroad between Wilmington and Jacksonville in North Carolina, as well as Highway US 17 which runs parallel with it for the greater part of its length. Here the soil and water conditions are very similar to the natural type and clearing operations favor good Dionaea development.

LOCALITIES OF SPECIFIC FIELD STUDIES

Combined with the attempt to relocate all reported stations for Dionaea, begun in the fall of 1954, was a search for habitats with large enough populations in suitable locations for detailed study. Reasonably extensive sites were needed for field experimentation and it seemed desirable that they have fairly distinct boundaries. Because daily observations were anticipated, the location had to be considered. During the summer of 1955 two such localities (Locations 1 & 2) were selected for study. Both were within 16 mi of the Duke University Marine Laboratory at Beaufort, N. C. (Fig. 3).

Location 1 (Fig. 4) was 0.5 mi south of Gales Creek on the west side of N. C. highway 24. It contained two stations (Z1 and Z2) within the Dionaea zones around the pocosins, and satellite station S1 in the savannah between. Location 2 (Fig. 5) was approximately 2 mi further south beside an unnumbered county road to Newport from N. C. 24. The site was about 0.5 mi from N. C. 24, just across a small tributary of Broad Creek and on the south side of the road. Here Station Z3 was set up within the Dionaea zone and satellite S2 in the savannah.

The two locations were similar in outward characteristics. Each was a small sandy savannah surrounded by a horseshoeshaped band of poscosin which was less than 2 ft lower in elevation. Both were representative of many similar areas in the vicinity. Species of *Zenobia*, *Lyonia*, *Ilex* and *Smilax* predominated in the pocosins with a few scattered pond pines. The savannahs supported longleaf pine and a ground cover of wire grass *(Aristida stricta)*. The ecotone between, marked by the addition of widely spaced, low ericaceous species, was the zone of Dionaea concentration. The longleaf pines of Location 1 were young trees, and very few were present, while those of Location 2 were mature and more abundant. Vegetational analyses and soil borings at both locations provided material for an idealized transect of the relations of the Dionaea ecotone (Fig. 6).

Fire had occurred in both locations during the spring of 1955, but there was no subsequent burning in the areas for the duration of the study except for the controlled experiments at Location 2.

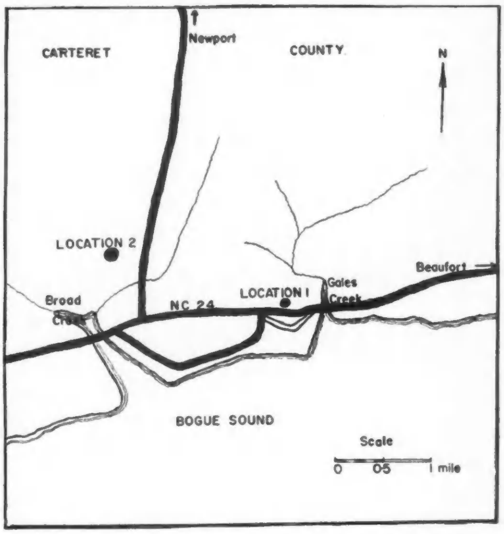

FIG. 3. The position of Locations 1 and 2 with respect to the highways and towns in Carteret County, N. C.

During the summers of 1955 and 1956 many other locations were visited so that generalizations drawn from the areas of intensive study would bear more validity.

CLIMATE

In a search for climatic factors of significance in determining the general range of Dionaea, analysis and comparison was made of temperature and precipitation records for several U. S. Weather Bureau stations within and outside the region where Dionaea grows. Actual measurements of microclimate were made at Locations 1 and 2 in the Dionaea zones and in savannah (Figs. 4 & 5). Temperatures were measured with Taylor sixes type maximum-minimum thermometers at 4 in. above the ground (shielded) and at ¼-½ in. below the surface. Evaporation was determined with paired black and white Livingston atmometer bulbs centered at a height of 6 in.

EVAPORATION

Readings were made at weekly intervals during the frost-free months of 1955 and 1956. Records from individual stations were so variable that valid comparisons could not be made among them. Consequently, only mean figures derived from savannah and zone stations must suffice for comparison.

No uniform distinction between savannah and zone stations was indicated by the excess loss of moisture from black bulbs when compared with white bulbs as wide fluctuations occurred with no apparent interrelationship. Since difference in evaporation between black and white bulbs is indicative of total radiation, it is suggested that the amount of radiation received

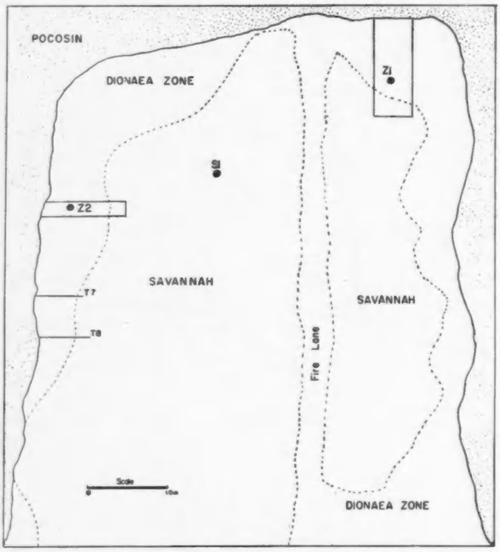

FIG. 4. Sketch map of Location 1. Dotted line is outer boundary of Dionaea zone; Z1 and Z2—zone recording stations; S1—savannah recording station; transects (T7-T8).

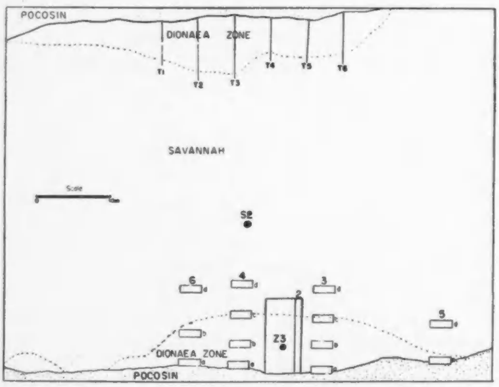

FIG. 5. Sketch map of Location 2 showing Dionaea zones, savannah and zone recording stations (S2 & Z3), positions of vegetation transects (T1-T6), cleared transect (2), and experimental plots (3-6 a-d).

in zone and savannah is similar. Therefore its effects as a differential factor at the two sites can be eliminated.

Water loss from white bulbs was about 25% greater in the savannah than in the zones. If radiation is equal in the 2 sites, then some other factor must account for the greater evaporation in the savannah. Wind velocity, as influenced by the height and density of the vegetation, is probably the major cause of this difference. Since the zone vegetation is generally higher and somewhat more compact than that of the savannah, and is sheltered by the still taller, heavier growth of the pocosin, wind velocity is reduced more in the zone area than it is in the savannah.

TEMPERATURE

Records were kept of maximum and minimum temperatures from July 1955 to mid-September 1956. The widest range of air temperature (94°F) was observed at a savannah station (S1) where the minimum was 21°F in December 1955 and the maximum was 115°F in July 1956. The widest range (92°) in a zone (Z1) was from 112°F in July 1955 to 20°F in December 1955. Since 1955 summer records are lacking for the savannah, absolute comparisons cannot be made. However, maximum temperatures in zone stations were slightly lower in 1956 than in 1955. Throughout the observation period air temperatures of both savannah and zone stations were very similar, except during the spring there was never more than 2°F difference in the respective maximum and minimum temperatures. In the spring, however, (end of March to beginning of June), the maximum air temperature in the savannah was up to 14°F higher than the air temperature of the zones.

Soil temperatures of the zone and savannah, on the other hand showed a more marked variation during most of the year, but especially during the spring when differences of up to 20°F between the respective maximum and minimum pairs were recorded. At these times the savannah instruments recorded the higher temperatures. During the summer the maximum soil temperatures in the savannah were seldom below 135°F while the zone maximum soil temperatures fluctuated between 110°-135°F. The ranges of soil temperatures were from 20°(Dec.)—135+°F (summer) in the zones and from 22°(Dec.)—135+°F (summer) in the savannah.

There is probably a definite correlation between the high evaporation rate and the pure sand soil of the savannah and its higher soil temperatures. The soil of the savannah dries out earlier in spring and more completely than the zones so that the savannah soil temperatures show a more rapid increase in the early spring and reach higher maxima.

PRECIPITATION

No measurements of precipitation were made because it was assumed that there would be little or no difference between the zone and savannah and conclusive records could not be obtained over a short period.

Within the Dionaea region, and to a distance of 50 mi from the outer limits, U. S. Weather Bureau records of 35 yrs duration or longer, were consulted. Snow rarely falls in this general area, and is more prevalent outside than within the range of Dionaea. During the year, rainfall at any one place is apt to be erratic, particularly during the summer, because of local convectional thunder showers, but over the years these irregularities become smoothed out. The mean precipitation for 12 stations within the Dionaea region was 49.95 in., while 6 stations outside the region had an average of 46.31 in. When precipitation for the

4 seasons was compared, it was found that the average spring precipitation of both areas is equal, while in each of the other three seasons rainfall is highest inside the Dionaea region. The maximum rainfall of both sets of stations occurs in the summer months (June, July, August), when more than a third of the total precipitation falls. South Carolina stations have higher rainfall than those in North Carolina, but there does not appear to be any general conclusion to be derived from this. Fayetteville and Southern Pines have rainfall totals which are more like coastal than inland records.

DISCUSSION

The temperature and evaporation data collected over the 14 month period during 1955-1956 do not indicate very great differences between the Dionaea zone and the surrounding savannah. Although temperatures at one of the savannah stations indicate slightly greater extremes than within the zones, the differences do not appear to be great enough to be directly effective in limiting the zone. It is clear that insolation, as determined by the differences in white and black bulb losses is not important. However, the greater evaporation rates in the savannah as determined by the white bulb data may be of indirect significance when related to other factors.

As shown in the studies of the soil, the depth of the water table increases and the amount of organic matter in the soil decreases progressively from pocosin to savannah, and it is in this aspect that the higher evaporation of the savannah is important in restricting the Dionaea zone. Water loss from the soil is greatly speeded up by the lack of ground cover and the presence of an almost pure sand surface soil, and from the plants, by the physical conditions favoring high transpiration rates. Replacement of water from below is slow and thus since the roots of Dionaea are so short, it is not able to compete successfully with such plants as Aristida.

The study of general meteorological records showed that average precipitation inside the range of Dionaea is slightly higher than outside. However, the difference does not appear to be sufficiently great to be of primary importance in delimiting the region, especially when it is realized that some of the stations just to the south of the range have a higher precipitation than those within the Dionaea area.

Various combinations of temperature were used in an attempt to find some correlation with the boundary, but without success. Studies of the climate within and without the range of Dionaea do not indicate an obvious factor which could be directly responsible for limiting its distribution.

SOIL STUDIES

CLASSIFICATION

The soils of the southeastern coastal plain included in this study have been developed chiefly from Pleistocene and recent sediments under the influences of a warm temperate climate with moderately high rainfall (50 in.), high ground water table and, to a lesser extent, fire.

The Klej-Leon and closely related soil series occurring primarily in regions of smooth relief, are the chief soils occurring in that region of the coastal plain where Dionaea is found. The chief soil forming the Dionaea substrate belongs to the St. Johns series, a ground water podzol (Lee 1955), as was observed in practically all borings taken at Dionaea sites. The soil profile descriptions for these sites were all very similar; most have a thin layer of peaty material at the surface, with a dark gray or black surface horizon, gradually lightening in colour with depth, overlying a coffee-brown cemented layer—the hardpan. Beneath this, the color varies somewhat from brownish-gray to almost yellow. Occasionally excessive wetness of the strata below 10 in. made it impossible to bring samples to the surface and prevented positive identification of the soil type. Otherwise all soil borings were regularly taken to a depth of at least 30 in.

PHYSICAL AND CHEMICAL ANALYSES

The profile of a 5 ft deep soil pit dug at Location 2 showed the characteristic development of the St. Johns series (hardpan soil), with a dark-coloured surface horizon gradually becoming lighter with depth and overlying, in this case, a yellow-brown sand. Plant roots were almost entirely confined to the top 3 in. with the few scattered in the next 10 in. mainly belonging to the various shrub species.

The physical properties were determined using samples from this pit and indicate the typical development of a ground water podzol in this region. In the hydrometer separation of sands, the total sands averaged between 93% and 98% at all depths and the total colloid content was no greater than 1.5% to 2.5%. Over 26% of the sand was retained in the 60 mesh seive while another 50-60% was retained by the 140 mesh seive. The moisture and xylene equivalents for the top 3.5 in. were 6.07% and 3.60% respectively.

Chemical analyses of the coastal plain soils indicate a very low level of fertility. This was shown by analyses of surface strata (top 4 in.) from the two Locations at Beaufort and from samplings near Edgecombe and White Lake. The analyses were made at North Carolina State College by Mr. Robert Schramm, using standard colorimetric methods. Although the samples were taken from widely separated areas, they were markedly similar in chemical composition. The most noticeable characteristics of these soils are the high acidity (pH 3.5-4.9), the complete lack of detectable calcium, manganese and nitrate, the very low amounts of ammonia (2 ppm), iron (1 ppm), magnesium (1 ppm), and phosphate (less than 2 ppm). The concentration of potassium at Locations 1 and 2 was 2 ppm which is equivalent to an agricultural rating of "medium."

Loss on ignition tests were run on soil samples (0-4 in.) collected from numerous Dionaea sites. The average percentage loss was 8.79% for 33 sites

with a range between 3.5 and 21.5%. Actually, most of the samples had less than this average loss and were remarkably similar. The high values were all due to the muck soils on which Dionaea is sometimes found.

SOIL MOISTURE

Moisture in the surface horizon of Dionaea zones is characteristic. Only during the late spring and summer do the better-drained soils, up slope from pocosins, dry to a depth of 2-4 in., but at all other times, the water content is high at the surface and the soil is obviously wet within 9 in. of it (water table). The depth to this wet soil varies with the depth of the hardpan and the proximity to the pocosin edge, as was demonstrated by borings taken at intervals across the zones from the pocosin edge into the savannah at Locations 1 and 2. At the pocosin edge the depth to the water table averaged 6.5 in. while at the margin of the savannah it averaged 13 in. The hardpan at the pocosin edge occurred at an average depth of 13.5-19.0 in. and at the savannah 19.0-26.0 in. The average percentage of organic matter decreased with increased distance from the pocosin (13.75% at pocosin edge to 5.31% at edge of savannah). This is to be expected since runoff and drainage increase up the slope, resulting in better aeration and hence more complete oxidation of the organic matter.

During the summer of 1955 soil borings were taken at intervals (3, 8, 12 m and 2, 6, 10 m) along the slope from the pocosin at Locations 1 and 2 (Z1-Z3, Figs. 4 & 5) to determine the rate of loss and degree of depletion of soil moisture during extended periods of dry weather. Unfortunately, dry periods were infrequent and of short duration so that the longest period of observation without rain was 12 days. Only two relatively successful series of determinations were made: one over a period of a week immediately after a rainy period, the other over a period of 4 days after a week of dry weather. Rain terminated the observations for both series. Although it was thought that rain did not occur during these times, and the stations were visited twice a day during these apparently rainless periods, it is possible that the not uncommon highly local showers may have contributed to certain fluctuations which appear in the data.

To compare these soil moisture data from the field with the potential amounts held under defined tensions, determinations were made of soil moisture in undisturbed samples at $\frac{1}{10}$, $\frac{1}{2}$, 1, and 15 atmospheres pressure. The lower pressure determinations were made with a porous plate apparatus and the 15 atmosphere determination on a pressure membrane extractor.

Using the mechanically determined soil moisture values as a basis, the field data indicated that although the moisture content of the upper 2 in. of soil showed some fluctuation all along the transect, the greatest was at the outer (savannah) edge where, at times, the tension was considerably greater than 15 atmospheres. At the inner area of the zone the soil moisture tension rarely was higher than 15 atmospheres and in general remained around $\frac{1}{3}$-$\frac{1}{10}$ atmosphere. The soils at the minus 4 in. level showed a much higher proportion of water, with nearly all of it being held at less than 1 atmosphere tension. Water is then readily available to the plant below the soil surface of the Dionaea zone if roots reach it. There is little apparent specific correlation, at least as determined in this study, between the amount of dry weather and depth of desiccation of the soil.

FIRE

Burning plays an important role in the development of the sandy soils of the Atlantic coastal plain and thus in the ecology of Dionaea. Although fire does not reach an intensity great enough to ignite sub-surface organic matter (Garren 1943) it is strong enough to burn off partially any surface detritus and thus aid in its further decomposition. The usual type of fire in the southeast is shortlived on any area and passes over the ground rapidly, burning most of the low vegetation in its path but without heating the sub-surface soil very greatly. Below 1 in. very little or no change in temperature can be detected (Heyward 1938). Most areas where Dionaea is found are burned fairly frequently and thus an A_0 horizon is almost completely lacking and the humus is incorporated in the A_1 horizon. The resulting sparse ground cover of frequently burned areas permits rain to wash the surface layers clean leaving a pure white sand, but beneath, the sand is dark gray because of the added humus and burned organic matter.

No comparative tests were made in this study of the chemical characteristics of burned and unburned soils. Available information is rather contradictory (Garren 1943) but most of the evidence indicates that burning decreases acidity and increases nitrogen, replaceable calcium and organic matter. The soils tested had all been burned recently and thus if the generalization is true for burned, uncultivated soils, then the unburned soils must contain an even lower proportion of nutrients, which may possibly contribute to the disappearance of Dionaea from unburned areas. Heyward (1939) showed in his comparative studies of burned and unburned longleaf pine forests, that moisture content was decreased in the upper 2 in. of burned soils. The peaty soil surface around the edges of a pocosin, because of its higher water holding capacity, probably is less affected by fire and thus contains less burned material.

From the study of the soils which are found in the Dionaea region, it can be stated that these plants are usually found on a medium to fine sandy soil containing some organic matter, either incorporated as humus in a manner similar to grasslands, or as an accumulation of peat. The amounts of mineral nutrients are low, but possibly not as low as they would be in the absence of fire. The soils generally have a high water content which is due almost entirely to the high ground water table and the ease with which capillarity can supply the upper soil levels.

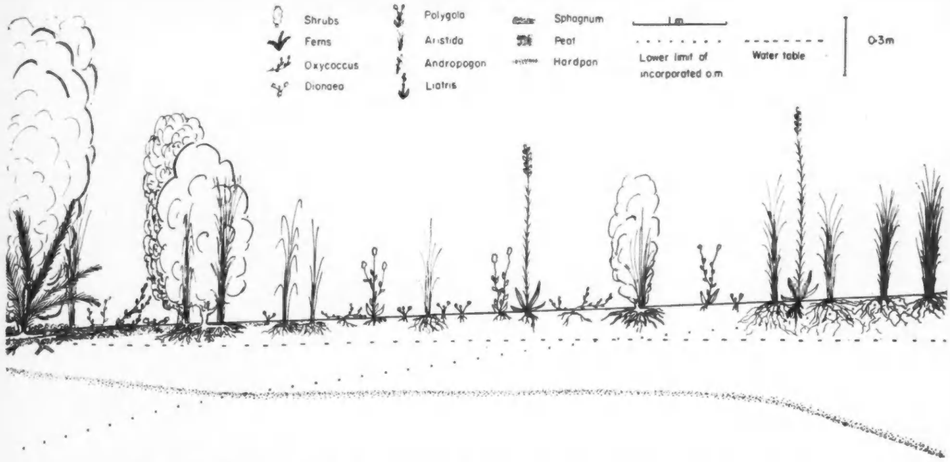

FIG. 6. Idealized bisect from pocosin edge with tall shrubs, to the grasses of savannah, and the relative position of water table, incorporated organic matter, peat and hardpan. Dionaea is shown in its relative position to other vegetation. Note difference in horizontal and vertical scales.

PLANT AND HABITAT

With the general nature of the habitat in mind, and particularly the physical factors involved, the field characteristics of Dionaea can be considered in relation to environment.

LOCAL DISTRIBUTION

As already pointed out Dionaea occurs in well-defined zones where changes in micro-relief are abrupt, and particularly this is true of the more northern habitats. Near Wilmington these zones or ecotones are much broader since the transitions between true pocosin and true savannah are commonly of far greater areal extent. Such wide zones are especially evident in Brunswick County between Wilmington and Southport, and in many of the large tracts of land belonging to the International Paper Company (especially in Pender and Horry Counties).

The relationship between slope and position of Dionaea in the field has already been referred to. A generalized diagram (Fig. 6) illustrates not only the change in the species composition up the slope, but also the change in peat, soil water, hardpan and organic matter relationships. Thus, it becomes clear that when the conditions of the zone containing Dionaea become more spread out, the plant will occupy wider areas.

Numbers of plants in the field vary widely. In some areas one is unable to walk without treading on them, while at other places they are so scattered as to be found only after careful search.

A plant census was made during the flowering season of 1956. Most of the data were collected at or near Location 1 and 2, but not within the designated study plots (Figs. 4 & 5). Counts were made of mature, immature and flowering plants on 20 randomly distributed plots 1 sq m in area (Table 1). Plants were distributed on the average of 89 per sq m, of which an average of 23 flowered. Throughout the study it appeared that flowering percentages of groups of plants were very low, and the census confirmed this observation, giving an average of 36-40% flowering for mature plants.

TABLE 1. Census of flowering and non-flowering Dionaea plants in undisturbed natural areas.

Location	No. sq m plots	Plants in all plots				Plants/sq m	
		Total	Mature non flowering	Mature flowering	Immature	Total	Flowering
1	11	920	421	281(40%)	218(24%)	84	25
2	9	843	321	184(36%)	257(30%)	94	20

EXTERNAL MORPHOLOGY

Although Dionaea has a complicated internal anatomy, its external morphology is relatively simple. It is made up of a short, unbranched, horizontal, white rhizome, surrounded by the fleshy bases of the leaves. The external form is that of an elongated bulb. From the lower surface arise 4-8 roots up to 15 cm in length. They are unbranched and bear long persistent root hairs. The rhizome lies in a slightly inclined position 2.5-4 cm below the soil surface, with the growing point at the lower end. The bilateral symmetry of the plant is masked by the radial arrangement of the leaves which is partly due to the way in which the youngest leaves ensheath the growing point. Fully developed leaves may be either prostrate or upright, depending on the season.

The age of a naturally grown Dionaea plant cannot be accurately determined. Although inspection usually serves to distinguish mature from immature plants, mainly on the basis of number and size of the leaves, the conclusion may not be valid. Many mature plants may sometimes produce immature-type

leaves, especially if the growing point has been injured. Development from seedling to mature plant is slow, a period of probably more than 3 yrs being required for an individual to reach the flowering stage. There are no growth rings or comparable age indicators. The number of leaves plus the number of persistent dead leaf bases may give some indication of minimum age but the rate of leaf base decay varies with size. Another factor to be considered is rate of leaf production which fluctuates under different conditions. In general, mature plants have fewer and larger leaves (4-8) than immature (10-16).

HABITAT ASSOCIATES

Common associates of Dionaea have already been mentioned but it should be emphasized that, although several species do indicate the likelihood of a suitable habitat, none can be designated as a reliable indicator of its presence.

Plant cover in Dionaea zones is characteristically sparse. The soil surface is generally completely bare between the individual plants, although at the pocosin edge Sphagnum is commonly present, forming dense mats. Vegetation is least abundant in the upper part of the zone and increases slightly from about the mid-point to the pocosin edge. Transects across typical margins (Figs. 4, 5) which were some 10 m wide showed only 26% cover in the upper 4 m with a slight increase to about 40% from the middle of the zone to the tall shrubs of the pocosin proper.

PHENOLOGY

Visible floral initiation is first apparent in the field early in April, and usually no further initials appear after the end of that month. Flowering begins about the last week in May and is usually over before the middle of June, although some plants may not finish before the beginning of July. Seed is usually ripe by the end of June, and dispersed by the middle of July. New seedlings first appear at the end of July and the beginning of August.

The terminal flower of an infloresence always opens first and immediately begins shedding pollen although the stigma is still immature. Approximately 24 hrs later the stigma is receptive, but by this time most of the pollen has been shed. Individual flowers, of the 8-12 in an inflorescence, open at approximately 24-hr intervals. Laboratory evidence indicates strict cross-fertilization. Self-pollination experiments did not result in seed production in a single instance. It is to be noted that Ellis in his letter to Linnaeus suggested that his plants did not set seed because of insufficient temperature, but it seems apparent now, that cross pollination was not effected. Presumably, pollination in the field is entomophilous, apparently by various beetles, small flies and possibly spiders, all of which may be seen in the flowers. Plants usually have a single inflorescence but occasionally two or even three flowering stalks are produced.

Seed dispersal is probably by rain drop splash. The ovate seeds stand, with the larger end upright, partially embedded in the placenta and a force greater than that of ordinary wind or alighting insects is needed to dislodge them. Thus, it is postulated that the beating of rain on the seed heads is responsible. At the time of the year when seeds are ready for dispersal, convectional thunderstorms with violent rainfall are common.

The distance of dispersal from the parent plant is not great, usually not more than a few inches from the base of the stem, as is evidenced by the proximity of seedlings to the parent plant. However, dispersal could be extended by rain wash as the seeds are light enough to be carried in small streams of water which often form during rain storms. Very probably this explains the occasional concentration of plants along the high water marks of depressions in areas which otherwise contain few or no plants.

Seedlings are usually found in protected sites in the field, most commonly around the base of mature plants but often in Sphagnum mats as well. They do not occur in open areas on bare sand where they would be subject to battering by rain, or to desiccation resulting from high insolation. However, where the soil is bare, but sheltered by overhanging, taller vegetation and has a thin surface layer of fine semi-decayed plant remains and humus, satisfactory germination and development can take place. These conclusions were drawn from field observation and from field sowing experiments.

Although growth is slow, development may sometimes be surprisingly rapid. Plants from seed sown in the field in July showed an average of 5 leaves per plant (range 3-9) in October. The same number of leaves per plant were present again in January, although it must be realized that some of the original leaves had died and had been replaced by new ones. During this developmental period all the leaves were yellowish in color, only the glands on the inside of the traps being red. By the end of the first year presumptive seedlings usually have 8-16 leaves up to 1 cm in length. At the end of the second year, the number of leaves remains about the same but they may be 1.5 cm long. However, it is dangerous to generalize as some plants, known to be 1 yr old, show the same amount of development as 2-year-old plants. Fig. 7 (N and O) illustrates the typical shapes of young leaves.

Seasonal variation in the size, shape and color of the leaves is quite apparent in the field. In the early spring most of the plants are green with petioles up to 6 cm in length and traps about 2 cm long. The leaves may or may not be erect. Usually if there is any red coloration noticeable, it is limited to the glands of the inner surface of the traps. The petioles at this time have a width of about 1.5 cm at the broadest part. With the appearance of the floral axis, leaf initiation usually ceases and no new leaves are produced until after flowering. These new leaves show a marked difference in morphological characters—they have long narrow petioles (up to 12.5 cm) which are nearly or completely wingless, upright in orientation, and bear traps up to 3.25 cm in

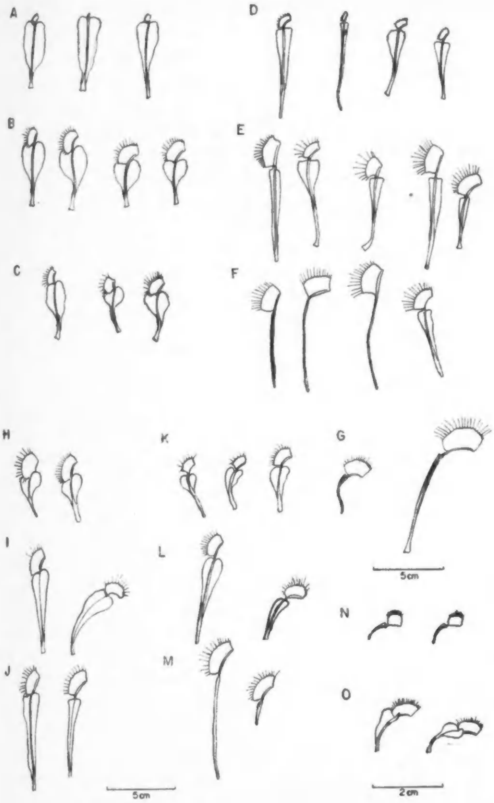

FIG. 7. Leaf morphology of laboratory and field plants as influenced by light intensity and photoperiod. A—G Laboratory-grown leaves: A—C 8-hr photoperiod, intensities (A) 50-100 fc, (B) 500 fc, (C) 1000-1100 fc. D—F 16-hr photoperiod, intensities (D) 50-100 fc, (E) 500 fc, (F) 1000-1100 fc. G continuous light, 500 fc. H—O field grown leaves: H—J shade leaves, (H) winter, (I) spring, (J) summer. K—M exposed leaves: (K) winter, (L) spring, (M) summer. Note: All leaves on same scale except N & O, leaves of 1- and 2-yr-old plants, respectively. See text for full description.

length (Fig. 7M). At this time the red coloration becomes intense, involving not only the glands, but also the tissue in between and often the marginal spines and petiole. Leaves of this nature are produced until the end of September when the winter type appears. This type is shorter, has a broader wing on the petiole and a trap smaller than the spring type. It is also prostrate and green and thus presents a marked contrast to the summer leaf type (Fig. 7K).

This description of the succession of morphological change in the leaf is necessarily generalized and hence exceptions do occur. These exceptions are apparently mainly related to water supply and to the extent of shading. Under heavy shade Dionaea leaves rarely, if ever, show red coloration, even in the glands. The leaves in the winter condition are typical of those just described—prostrate, wide-petioled and with small traps (sometimes the leaves may be somewhat longer than is typical, Fig. 7H). However, during the summer, although the length of the leaves is equal to that of the spring type, they are generally prostrate, or slightly decumbent, and have petioles only slightly narrower than in the winter (Fig. 7J).

The shape of the individual trap is to some extent an indication of the maturity of the plant. Comparison of leaves of different ages indicates that besides the difference in the size of the traps (not a reliable guide) the general shape is different, the leaves of very young plants (Fig. 7N) being somewhat square in outline, while the leaves of older plants are almost reniform in shape (Fig. 7).

DISCUSSION

It is inferred from the climatic data that the climate is so similar within and beyond the range of Dionaea that, as such, it does not play a major role in delimiting the zonal areas or the overall boundaries of its occurrence. Nevertheless, the general climatic characteristics within the range play a very important part in the life history of Dionaea. The high summer rainfall is probably of great significance, since it tends to keep humidity high and thus to ameliorate drought conditions especially during germination which occurs in the hottest months. (Moisture content of the soil as shown later is an important influence in the seasonal changes in leaf morphology.)

The plant material produced in the savannah during the summer is still present the following spring, and as a result of low spring rainfall, dries out rapidly. This dead, dry material, being highly inflammable, is primarily responsible for the prevalence of fire at this time of year. Because fire appears to be of some importance in the occurrence of Dionaea and in maintaining favorable habitats, some attempts were made to clarify its effects. The results appear in the experimental section.

The chief differential climatic factor between the zones and the savannah is apparently wind as reflected in a differential moisture loss from atmometer bulbs in the two sites. Hence, greater air movement in the open savannah must contribute to the faster drying of its surface soil.

One of the main factors delimiting the total range of Dionaea appears to be water. Comparison of field moisture determinations with the laboratory determined field capacity ($\frac{1}{10}$ or $\frac{1}{3}$ atmospheres) and the wilting percentage (15 atmospheres) shows that the top 2 in. of soil of the low inner margin of the zone rarely reached the wilting percentage, while soil at the outer margin often developed greater moisture tensions. Soil moisture tensions greater than 1 atmosphere seldom occurred at deeper levels. These determinations were made in the summer when possibly the soil does not dry out completely, so it is suggested that higher tensions may be developed during the spring. Thus it is likely that this season may impose the greatest limitation on the survival of

mature Dionaea at the outer boundary of the zone. Seedling tolerances are also important in the delimitation of the zone. The requirements for field germination are not generally met on the bare, highly insolated sand of the savannah and hence seedlings establishment is precluded.

The structure and composition of the soil (chiefly St. Johns Series) were shown by the analyses to be very uniform throughout the Dionaea range. The predominantly sandy nature of the soil together with the high proportion of surface organic matter and the proximity of the water table to the surface were characteristic wherever Dionaea was found. The limits of specific habitats of Dionaea appear to be due to local topographic differences resulting in alteration of soil and moisture relationships.

EXPERIMENTAL OBSERVATIONS

FIELD EXPERIMENTS

BURNING

It has already been indicated that fire may have a large influence on the growth rate of Dionaea in the field and on its survival in a particular area. Thus, certain experiments were carried out in the field to determine what effects of burning were most influential on plant growth.

Four series of plots (each 3 by 1 m) were spaced along lines traversing the Dionaea zone at Location 2 (Fig. 5) in July 1955. One plot in each series was at the edge of the pocosin and one at the edge of the savannah. Plots between were, presumably, representative of average Dionaea habitats. All surface vegetation was removed from 2 sq m of each plot and the refuse was collected and burned. The ashes and charcoal were reapplied to 1 sq m of the cleared portion of each plot after it had been burned over with a blow torch. A week later, Dionaea was transplanted from a nearby site into each section at the rate of 40 plants per cleared meter (one with ash, one without) and 20 per uncleared. The plants were marked with stakes and left, their further development being observed for the following 18 months.

Not until flowering occurred about 10 months later were the first obvious differences noted (Table 2). The plants in the cleared plots all flowered slightly earlier than in the uncleared or in the natural areas, and the flowering percentage in the cleared areas was higher (overall average on cleared, burned and unburned plots, 68%, uncleared plots, 51%). The figures for the burned and unburned plots are somewhat variable, but the overall averages show a higher percentage of flowering in the burned plots (72%) than in the unburned (64%).

The low figures for the uncleared plots are in general higher than those obtained in the natural areas (the average figure of the natural areas being 38% and for the uncleared plots 53%). The discrepancies in the figures which appear for the cleared areas, are unexplained, but the variation in cover and competition could be responsible, especially in the D plots (savannah). Here the plants in the uncleared sections of 4D and 6D (higher flowering percentage) had less competition than in the corresponding sections of 3D and 5D (lower flowering percentage).

After flowering, some differences became apparent between the paired sets of treatments on cleared portions of the plots. Those plants on the burned plots looked healthier, but the differences were of a qualitative nature and may have been caused by other factors. Although the responses in the experimental plots contributed no startling new information they do support observations made on burned areas elsewhere. Within 2 yrs after burning, plants in such areas are invariably more vigorous than plants in adjacent unburned areas.

Supplementary information on the effects of fire was gained by burning off all surface vegetation, including Dionaea, from undisturbed blocks of soil brought in from the field. Resulting temperatures did not kill the growing points of Dionaea, as new leaves appeared within 2 weeks after burning. The Dionaea plants in the blocks of soil treated in this manner showed visible floral axes earlier and were more vigorous than plants in similar unburned blocks. Thus, the stimulating effect of burning must either result from the release of nutrients into the soil in a more available form as suggested by Garren (1943), or it must be by reduction of competition. On the basis of the field experiments and observations, it appears that the latter is the more obvious explanation, but the nutrient angle cannot be neglected.

Although the rhizomes of Dionaea are in the top 2.5-4 cm of soil, the larger ones are well protected from fire injury, and the roots, being deeper, are unlikely to be affected. This may be deduced from the temperatures, recorded by Heyward (1938) for the soil heating effects of forest fires in longleaf pine areas. The surface soils of Dionaea zones being moister, the temperatures during burning are likely to be lower than those obtained in the longleaf soils.

TRANSPLANTING

The series of plots used for the burning experiments was also used to make other observations. A comparison was made of the size and vitality of the transplants within the normal range of the zone and at its extreme margins (Fig. 5).

There were several clear-cut differences in the vigor of the plants. Within the zone the diversity among plants was no greater than the individual variation to be expected in any population. However, the plants in the savannah (D plots) showed a distinct retardation in vegetative development in the spring of 1956. They were much more compact and less developed than those within the normal zone. The spring was moister than usual for the region, no fires occurred in the area of observation; the summer of 1956 was also wetter than usual, although no hurricanes occurred that year. Still, plants in the savannah plots had a mortality of 9%, compared with only 0.25% for those in all other plots. Had the spring and summer been drier, it is probable that the

TABLE 2. Flowering percentages in transplant experiment.

	UNCLEARED			CLEARED AND UNBURNED			CLEARED AND BURNED		
Quadrat	Total plants	No. dead	% Flowering	Total plants	No. dead	% Flowering	Total plants	No. dead	% Flowering
3A	20	0	65	40	0	75	39	1	41
4A	20	0	40	40	0	80	40	0	55
5A	20	0	15	40	0	58	40	0	60
6A	20	0	70	40	0	90	40	0	90
			Av. 48			Av. 76			Av. 62
3B	20	0	50	40	0	68	40	0	43
4B	20	0	20	40	0	70	40	0	75
6B	20	0	70	40	0	50	40	0	80
			Av. 40			Av. 63			Av. 66
3C	20	0	64	40	0	65	40	0	72
4C	20	0	70	38	2	47	40	0	95
			Av. 67			Av. 56			Av. 84
3D	18	2	44	39	1	56	31	9	65
4D	20	0	85	40	0	75	40	0	100
5D	17	3	29	38	2	58	38	2	71
6D	16	4	75	34	6	53	34	6	71
			Av. 58			Av. 61			Av. 77

A=pocosin edge
B=lower area within zone
C=upper area within zone
D=savannah

mortality rate would have been higher, although the plants may have gone into a dormant condition.

Although the plants in the cleared plots flowered earlier than those in the uncleared plots, the savannah transplants flowered a little earlier than the rest of the plants in the transplant experiment. The flower stalks in general were shorter in the D plots than nearer the pocosin, with fewer flowers per inflorescence. It has already been noted that the plants in the uncleared D plots with greater competition showed lower flowering percentage than those in the lower-competition uncleared plots. However, in contrast, the low flowering groups (3D and 5D) were more vigorous (vegetatively) than the high flowering groups (4D and 6D), but all plants of the uncleared D plots were much more vigorous than those in the cleared D plots.

On the other hand, plants of the uncleared areas of the other plots were all smaller than in the cleared areas, and this difference was more noticeable the greater the intensity of shade and competition from over-hanging vegetation. Most of these shaded plants retained winter or spring leaves through the summer. In relation to water, the plants growing in micro-depressions were more vigorous than those on slight ridges, particularly in the drier plots. At the inner edge of the zone the effect of the greater amounts of water was mainly apparent in the type of leaves produced by the plants growing there: although upright leaves were developed, in general they were winged. Plants of the drier areas produced narrow petioled summer-type leaves (Figs. 8 & 9).

Flowering of the plants of the inner plots (A and B plots) was greater in the cleared than the uncleared areas (Table 2).

One other plot, 0.5 m in width and 10 m in length running parallel with the transect plot containing Z3 at Location 2, was completely cleared of all vegetation except the flytraps, but the surface soil was left undisturbed. The important difference which appeared in this cleared plot was in the relative sizes of the plants. The largest plants were at the pocosin end, and in general, had the largest leaves and the longest flower stalks. Flowering percentage was higher throughout this plot than in natural areas.

An interesting confirmation of these transplant experiments was gained when a visit was payed in January 1957 to Mr. Aubrey Shaw of Lake Creek Community, Bladen County, who had transplanted Dionaea into several locations showing obvious physical differences from the natural habitat. The transplants were made in 1950 as follows:

1. Dry area
2. Heavily shaded area
3. Moist area
4. Shallow drainage trough (high pH)
5. Submerged in a pond.

1. The dry area was in an open cut-over longleaf pine savannah. The surface soil of this savannah becomes almost completely desiccated in summer, and, as a result, these transplants have two growth cycles during the year. It was reported that after the first surge of spring growth, the plants became completely dormant for the summer months, then produced new leaves toward the end of the summer or

FIG. 8. Transplants in unburned soil (quad. 6B) which have generally upright leaves with very narrow petioles. The short, prostrate spring-type leaves were formed prior to floral initiation.

the beginning of autumn after the heavier rains began. No flowers had been produced, the dormancy setting in about the time of initiation of the floral axis (April). The area where they were transplanted had several ridges and hollows; those plants in the slight hollows were more vigorous than those still alive on the ridges. Mortality had been heavy in this group of transplants. At the time of observation, all the plants in this area were small, green in color and in typical winter condition.

2. The shaded area was at the edge of a trail through a pocosin where the soil was very wet, and where leaf litter from the overhanging shrubs had built up a thick mat of semi-decayed mold. During the winter and probably during the summer as well, the plants are unable to produce leaves of sufficient length to penetrate the overlying litter. Only a few of these transplants had survived, and none had flowered. Their leaves were green, prostrate, broad-petioled, without traps and of a thin papery texture.

3. The moist area was in a position on higher ground than area 2, but close by, without the shade factor and with very little competition. These plants were very healthy, and had prostrate leaves of a deep red color and broad, very short petioles. Dead

FIG. 9. Transplants in unburned soil (quad. 6A). New leaves with petioles all broader than in Fig. 8 because of excess moisture available in quad. 6A.

leaves gave evidence that some upright leaves had been produced during the summer. Flowering occurred in 80-90% of the plants in 1956, and a good crop of seedlings was present.

4. The shallow drainage trough, which originated in a cultivated field, was always wet but seldom carried a large volume of water. The soil was less acid (pH 5.5) than is normal (pH 3.8-4.5) in Dionaea habitats. The plants here were large and the leaves green, but the glands showed a slight red coloration. The leaves were more typical of the spring than the winter type, with long, winged petioles and medium-sized traps. The plants had flowered in 1956, and the seedlings were larger and relatively more abundant than in area 3. It was reported that the "catch rate" of these plants was relatively high, and many of the traps investigated showed the remains of partially digested beetles, woodlice and planarians.

5. The submerged plants had been completely under water for 7 yrs and were still very vigorous. At times the traps of some leaves had been above the water level, but the growing points and petioles had always been submerged. There had been no flowering during the time of submergence. All plants were in an extreme spring condition, displaying very long petioles (13-15 cm) and traps (4.25 cm). Planarians, mayfly and other aquatic larvae and even newts were seen in the traps in partially digested state. Most of the traps examined contained either newly trapped animals or the remains of digested ones. Thus, the trap mechanism is not only sensitive under water, but is able to close with sufficient rapidity to catch fast-moving aquatic animals.

Prior to the visit to Mr. Shaw, flooding experiments had already been completed in the greenhouse. Mature plants had been kept continuously flooded for 3 months without injury. Immature plants which had

been in water-logged soil for 7 months remained large and healthy, and some produced flowers. Soil conditions of the plants in Mr. Shaw's field area 4 and of those in the water-logged soil of the greenhouse were similar.

The plants in the natural areas of Lake Creek Community were similar to those in the drier parts of Locations 1 and 2. The flowering ratio, as far as could be determined, was similar to that in the study area, and seedlings were present. In one small region, the competitive vegetation had been kept at a minimum, and the plants here had produced more flowers than those under completely natural conditions. Fire had not occurred in the area for about 15 yrs, and this may partly account for the small size of most of the plants. Dionaea in this region was scattered over a wide area of semi-savannah, mainly at the edges of slight depressions containing a heavy growth of low ericaceous shrubs.

SHADING

At Locations 1 and 2 in January 1956, 4 areas (containing a total of 188 mature plants) were shaded with layers of cheesecloth which reduced the light intensity by about 50%. About 40% of the plants developed obvious floral initials but an average of only 15% of the total number of plants flowered (7.6% at Location 1 and 23% at Location 2), indicating high mortality among these initials. No comparative counts were made of the dead initials in the natural areas because the observed scarcity did not appear to warrant it.

The floral axes of the shaded plants reaching maturity were badly bent, even though not touching the cheesecloth, and the flowers were atypical, malformed and set no seeds. Most of the plants remained in winter or spring condition through the summer of 1956, and showed a more marked development of the winter condition in 1956-57. During the summer the plants were somewhat etiolated and prone to insect attack. It was readily observed, in all areas visited that, under heavy shade, plants did not produce as many flowers as in the open; this was substantiated in the transplant experiments already described.

FLOWERING

General observation suggested that flower production is not correlated with such morphological characters as size, and number of leaves. After apparent maturity, measurable characters appear to be equally distributed among flowering and non-flowering plants alike. Consequently, within Locations 1 (Z1) and 2 (Z3), flowering plants were staked in 1955 so as to be recognizable in 1956. These plants when counted the following year showed about the same proportion of flowers as in the wider census, the average being 40%. However, there was a considerable difference between the percentages at the two stations, the higher being at Location 2. This difference was also apparent in the shading experiments. Direct comparison with the wider census figures cannot be made as these were taken from a larger area than the designated stations.

The differences in the percentage of floral initiation and flowering at Locations 1 and 2 are possibly related to the occurrence of fire in these areas. Although fire had occurred in both areas in the spring of 1955, it appeared to have been more effective in burning surface vegetation at Location 2 than at Location 1.

One interesting fact emerges from these studies, namely, that although greenhouse (as reported later) and natural field populations show a low flowering percentage which is apparently not directly correlated with size, vigor, or the production of flowers the previous year, plants which were transplanted to cleared plots, or in areas from which the other vegetation had been removed, showed a considerably higher proportion of flowers. Absence of competition is not the only factor, or flowering in the greenhouse should have been in higher ratios.

DISCUSSION

The field experimental studies on Dionaea to a large extent were not conclusive but do point up important factors affecting the presence of Dionaea in local habitats. Fire has been shown to be important at least to the extent that it eliminates competition and thereafter allows more vigorous growth of Dionaea. The temperatures generated during surface fires are not injurious to mature plants. Although the leaves are killed, the rhizome is apparently unaffected and new leaves appear rapidly after fire.

Burning also removes accumulated litter, which effectively excludes Dionaea from a site if it becomes too deep. Where the deep litter collects in wet areas, establishment of Dionaea is prevented.

Heavy shading reduces floral maturation, although apparently it does not affect floral initiation to any great extent. Thus, in areas where Dionaea has become established, elimination of fire and the consequent development of heavier growth of associated species will reduce flowering and hence, eventually, the population will become entirely eliminated. One example of such a phenomenon in progress is in an International Paper Company's loblolly plantation at Edgecombe. Evidently at the time of planting the pines, there was a large and vigorous population of Dionaea, but since then with protection from fire, the grasses (mainly Aristida) thrived and formed a very thick ground cover. This cover reduced floral maturation and the plants have lost vigor so that the Dionaea population will probably be seriously reduced or even eliminated over a large section of that area.

Another factor shown to be of importance in the production of floral initiations is the duration and time of the driest season as well as the extent to which the soil dries. Thus, although Dionaea can survive periods of severe desiccation by going into dormancy, floral production is prevented if the dry

period comes in spring, and germination and establishment of seedlings are prevented if the dry period comes in the late summer or fall. However, if sufficient organic matter is incorporated in the soil, allowing greater amounts of water to be held, and if the water table is sufficiently high, the effects of the dry period are considerably reduced.

LABORATORY EXPERIMENTS

WATER RELATIONS

Although determinations made during the summer show that the soil moisture of the Dionaea zone rarely falls to the permanent wilting percentage, there are times when soil moisture stress may be an important limiting factor at the outer limit of the zone. Thus it was considered desirable to determine the ability of Dionaea to dry out the soil and to withstand severe moisture stress.

Since the root system of Dionaea is poorly developed, and growth of the plants is slow, the conventional method of testing the permanent wilting percentage of the soil (PWP) was not followed. The root systems of mature plants were placed in glass tubes (4 in. long, 0.5 in. in diam.) and air dry A horizon St. Johns Series soil poured in. The base of the tube was covered with a double layer of cheesecloth to prevent loss of the soil and to allow drainage. The tubes were then immersed in water until the soil was saturated, and buried up to their necks in sand for 4 weeks to allow the plants to recover from transplanting. At this time the tops of the tubes were sealed with vaseline (around the base of the plant leaves) and the whole tube wrapped in aluminum foil to prevent loss of water by evaporation and possible light damage to the roots.

The experimental plants were left in a sunny position in the greenhouse and weighed each morning. Permanent wilting (youngest visible leaves were wilted in the morning) occurred within 2 weeks. Each plant was then removed from the tube and a soil sample taken from around the roots (roots removed) for determination of moisture percentage by oven drying. The experimental plants, consisting now only of rhizome and roots, were placed then in a favorable environment to recover.

To determine the availability of the water present in the soil used, when the plants wilted, a 15 atmosphere moisture determination was made with the pressure membrane extractor. A conventional determination of PWP of this soil was also made using sunflower. To insure growth of sunflower in St. Johns soil, the acidity was adjusted to pH 6.5 by the addition of calcium hydroxide.

Results indicate that both Dionaea and sunflower are able to dry out this soil below the mechanically determined 15 atmosphere tension (5.31%). The PWP of the soil using Dionaea as an indicator was 3.38%, and sunflower was 3.73%, but the difference between these two is probably not significant.

The amounts of moisture lost by Dionaea were highest at first (0.83 gm in first 2 days) but dropped off rapidly (0.192 gm on 6th day, 0.052 on 14th day). This rapid drop in moisture loss was probably caused first, by the loss of water from the soil immediately around the roots, and secondly, by the early wilting of mature leaves and cessation of growth by the immature leaves as a result of moisture stress. The very small amount of water loss just prior to PWP (0.052 gm) can be attributed to the almost complete elimination of the transpiring surfaces (due to permanent wilting and/or death of the mature leaves).

When, after severe desiccation, these plants were placed in a favorable environment, new leaves began to appear within 2 weeks and almost 100% recovery followed. Apparently sufficient reserve material is stored in the swollen leaf bases to provide for rapid new growth after the return of moist conditions.

Further confirmation of this type of reaction in Dionaea was found when a number of individually potted plants were sealed off to prevent any loss of moisture except through the leaves. After 2 months, signs of severe drought were apparent, growth had ceased and all leaves had died. However, several of the plants later initiated new growth, although no water was added. The plants showing this new growth survived for approximately 6 months; this second growth was very slow, and the new leaves were small and very leathery, without traps. When examined later, it was seen that only the largest rhizomes had produced the second growth. Mature plants are able to withstand several periods of alternating severe drought and good water conditions without going into dormancy, while immature plants will not survive.

Studies such as these, as well as the report of the dry transplant area of Mr. Shaw, suggest that the rhizome with its surrounding swollen leaf bases is extremely important in allowing Dionaea to withstand periods of extreme dryness.

SOIL TEXTURE

As already described, the native soil of the southeastern coastal plain is mainly sand with a certain amount of burned and unburned organic matter incorporated into it, is very acid and of low fertility. In investigating the range of tolerance of Dionaea to varying habitat conditions, different soils were used to determine their effects on general growth and flowering. Two experiments were designed, one using plants taken from the field not long before floral initiation occurred (March 1956), and the other using plants collected at the end of the summer (September 1956).

In the first experiment, 12 large, vigorous plants were transplanted into flats containing the following soils:

Flat 1. Natural coastal plain soil
Flat 2. A local clay-loam garden soil
Flat 3. A specially prepared greenhouse potting soil
Flat 4. Washed white sand
Flat 5. Pure peat moss

All flats were placed together in the greenhouse and watered with distilled water. Only 11 days elapsed before floral initiations were noticed and after the 23rd day no more initials developed. The only instance where all plants developed visible initials were those in Flat 2, but 11 initials appeared in the plants of Flats 1, 4 and 5, and 7 in plants of Flat 3.

However, after initiation, responses varied. Within 30 days of transplanting, differences in the general leaf coloration and shape were apparent. In Flat 4 the traps began to develop a deep red color. Plants in Flats 1 and 2 showed the same trait but to a lesser degree, while the plants in Flats 3 and 5 remained green. These differences became more apparent with the development of deeper coloration in the traps of plants of Flats 1 and 4; only the glands became red in the plants of Flat 2, giving the traps a pinkish color; those in Flats 3 and 5 remained green, although the plants in Flat 5 were much darker than in Flat 3.

The floral initials, although appearing approximately at the same time, did not develop at the same rate and many did not reach maturity. After 41 days only one initiation was still alive in the greenhouse potting soil (Flat 3), and 3 of the plants had died. This remaining initial flowered 44 days after its appearance, but the flower stalk was extremely stunted, the stem twisted and bent, and the inflorescence poorly developed with only a few malformed flowers. Although the flowers of this inflorescence were crosspollinated, no seeds were set. Differences appeared in all the flats which could apparently be related to the soil type in which the plants were growing. The most prominent differences are summarized below:

Flat 1. Natural coastal plain soil: All plants bloomed within 49 days of their initiation, although 2 plants did not reach maturity owing to accidents with flowering shoots. After flowering, all plants developed normal summer-type leaves with the characteristic red coloration.

Flat 2. Local clay-loam garden soil: Flowers of 4 plants finally reached maturity within 46 days of floral initiation. Thereafter, the plants showed little vigor, the leaves remained very leathery and of the late winter type. In general, the leaves did not develop traps.

Flat 3. Greenhouse potting soil: One plant flowered within 44 days and died shortly thereafter. All other plants died within 70 days of the time of transplanting.

Flat 4. Washed white sand: All initiations reached maturity within 47 days. After flowering, vigorous growth occurred with the production of summer leaves and red coloration.

Flat 5. Pure peat moss: All initiatious reached maturity within 48 days. After flowering, the plants remained in typical spring growth condition, with broad petioles and small traps.

TABLE 3. Flowering data from plants in soil texture experiment.

Flat		1	2	3	4	5
Soil		Native	Garden	Green-house	Sand	Peat
Number of	Plants	12	12	12	12	12
	Initials	11	12	7	11	11
	Flowers	9	4	1	11	11
Aver. Time in Days Until	Appearance of initials	16	17	19	16	16
	Opening of first flower	44	44	44	43	44
	Opening of first seed pod	33			32	33
Range in Time for	Initiation	15 Mar-24 Mar	19 Mar-26 Mar	20 Mar-27 Mar	16 Mar-25 Mar	19 Mar-25 Mar
	Flowering	24 Apr-6 May	30 Apr-4 May	3 May	29 Apr-7 May	30 Apr-8 May
	Seed ripening	29 May-10 June	....	....	29 May-10 June	30 May-10 June
Aver.	Flowers per inflorescence	6	3	2	9	6
	Length of floral axis (cm)	20.7	11.8	5.8	20.1	19.2

Table 3 summarizes the development of the plants used in this experiment.

When the experiment was finally concluded after 5 months, all plants in Flats 1, 4 and 5 were alive and very vigorous although the plants in Flat 4 were much larger than those of the other two. In Flat 2 only two plants were still alive, and were very unthrifty. These were taken from the soil and the roots washed. The probable cause of their low vitality was immediately apparent—there had apparently been no new root growth during the whole time of the experiment. Each plant had 4 roots and not one was more than 4 cm long. In contrast, plants removed from the other flats, each had 6-8 well-developed roots which averaged 3-5 cm in length (in Flats 1 and 4), and 15-20 cm in length (in Flat 5).

This experiment indicates that soil differences do influence the rate and type of development of Dionaea. At first, the sudden rise in temperature from the field to the 72°F greenhouse was probably responsible for the speed of appearance of the initials without any affects from the soil itself. However, after a time, the health and vigor of the plants reflected the soil type, with a decline in those plants in pure mineral soil (possibly the speed of decline in Flat 3 was partially due to the fertilizer added in the preparation of that soil), which led to coloration changes, loss of initials, loss of fertility, and finally, death. The explanation appears to lie in the fact that root growth is suppressed in the heavier soils. The higher pH and nutrient content of the artificial soils are probably contributory.

A second experiment involved the use of different proportions of sand and clay as the substratum for

Dionaea. Transplants were made in September, 1956, and carried through to January, 1957. Mixtures of clay (Georgeville, a kaolinite type) (100%, 75%, 50%, 25%, 0% by volume) and sand were made and duplicate flats of each mixture prepared. Thirty mature Dionaea were planted in each flat as well as ten 2 to 3-yr-old plants.

Results of this experiment were unexpected, as the plants in the lower proportions of clay were as slow in growth as those in the higher, and generally died off more quickly. Georgeville clay has been shown to contain a high percentage of mineral nutrients, which may be the reason that all plants did poorly. The young plants all died within a month of planting, while plants in the flats with 25% and 50% clay had all died within 2 months. At the end of the experiment, only 10 plants were alive in the 100% flat, and 15 in the 75% flats. The plants in the sand flats all grew normally.

NUTRIENT EXPERIMENTS

Knowledge of the nutritional requirements of Dionaea would probably shed some light on the range of its habitat demands, and might provide a partial explanation of its endemism. Early investigators were intrigued with the problem of capture and digestion and Canby (1868) foreshadowed in his paper the nutrition work of Darwin which appeared in 1875. The following year, Balfour (1876) also published results of digestion experiments. Curtis (1834) had remarked, "It is not to be supposed that such food [insect] is necessary to the existence of the plant, but like compost, may increase its growth and vigor." The other early workers had similar views, with Sachs (1887) suggesting that animal substance not only improved vigor, but those plants prevented from "feeding" remained small and did not flower. De Candolle (1876), on the basis of his work (6 week experimental period), concluded that absorption of animal material was unnecessary for normal development. Tate (1875) had already come to the same conclusion for Drosera.

In spite of all the discussion in the early literature, no definite conclusions can be drawn concerning the role of animal matter in the life cycle of Dionaea except that further investigation of nutritional responses is necessary. Consequently, preliminary studies of both the mineral and organic nutrition of these plants were begun.

Nutrient solutions (modified from Burkholder & Nickell 1949) and a dilute Hoaglands solution were the main mineral solutions used, and a yeast protein extract and *Drosophila melanagaster* were the sources of organic nutriment. The mineral solutions were supplied through the soil and through the leaves, and the organic material through the leaves only. Plants were grown in washed sand. The seedlings were germinated in the laboratory and the older plants were obtained in the field.

Details of the exploratory experiments would not be justified in view of the inconclusive results. The generalizations suggested by the work indicate that intensive study along these lines would yield rewarding information. All plants receiving mineral nutrients grew poorly, while all the controls (watered with distilled water) showed much more satisfactory growth. The mature experimental plants steadily declined in weight, and died after about 3 months. Growth of all plants whether experimental, control, or in normal soils of the coastal region, was very slow, and this fact prevented further experimental work in the time available. The plants which were "fed" organic material, on the other hand, showed more vigorous vegetative growth. None of the plants under the various nutritional regimes flowered in the season following the experiments, while approximately the same proportion (45%) of the control plants flowered as was noted in the field (40%). It is probable that poor growth of the experimental plants resulted from using too high a concentration or the wrong proportions of nutrients.

FLOWERING

The variability of flowering responses in several experiments and the fact that only about 40% of mature plants flower in the field indicated a need for study of possible influencing factors. Since floral initials were first apparent in the field in April, it was postulated that production of flower buds in Dionaea is a photoperiodic response. A supporting reason was that field studies, already reported, had indicated the importance of light intensity as a factor controlling development of floral initials.

To test this hypothesis, a combined light-intensity-photoperiod experiment was designed in which plants (collected from the field in early January 1956) were placed in daylengths of 24 (continuous light), 16, and 8 hrs. Temperature and humidity were controlled in the 24 hr regime, the former at 72°F and the latter at about 45%. Both the other regimes fluctuated according to the temperature and humidity of the building. Forty plants in each regime were exposed to a light intensity of 500 fc, and the 2 shorter regimes also had groups of 40 plants under light intensities of 1000-1100 fc and 50-100 fc. When the flowers opened, they were all artificially cross-pollinated (if pollen was available) by use of a camels-hair brush.

Not only did the times of appearance of the floral initials differ in the various groups, but also the final percentage of flowering (Table 4) and the general leaf morphology.

Within a month after starting the experiments, morphological changes were noticeable in leaves initiated after exposure to the new light regimes. Some of the changes were very gradual, requiring 4-6 months to attain the final type of leaf. In part this was probably due to the habitat from which the plant was taken and also to its maturity at the time of transference. Figure 7 shows the early types of leaves produced and the final types, if these were

TABLE 4. The effect of daylength and light intensity on flowering.

Day-Length (hrs)	Light Intensity (f. c.)	Number Plants	Number Initiating	Number Flowering	Initiation Dates	Average Days Till Flowering	% Flowering	Seed Set
24	500	50	16	16	16 Feb-26 Sept	56	32	+
16	1000-1100	40	17	16	25 Feb-13 Mar	27	40	+
16	500	40	6	3	29 Feb-13 Mar	37	8	+
16	50-100	40	11	2	7 Mar-17 Mar	45	5	0
8	1000-1100	40	5	5	26 Feb-11 Aug	32	13	+
8	500	40	3	3	21 Feb-10 July	39	8	+
8	50-100	40	4	1	28 Jan-6 Mar	60	2	0

markedly different. Descriptions are given separately for each daylength regime.

1. *The 24-hour photoperiod* (Fig. 7G). (500 fc only). Leaf type stabilized rapidly to typical open field, summer form; petioles all wingless, some long, some short; traps generally larger and deep red (spines, glands, leaf tissue), color often extending on to petiole; some plants (long or short-petioled) devoid of red color, were usually yellow green as also observed in the field—possibly genetic or due to nitrogen deficiency. All plants developing visible initials (32%) produced flowers and viable seed when pollen was available for cross-pollination. (Fig. 10, #308 shows flowering plant before typical leaf type developed).

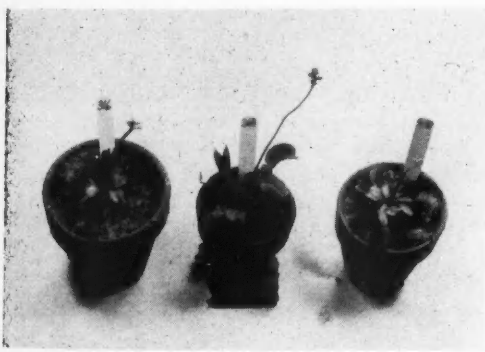

FIG. 10. Plants grown under medium light intensity (500 fc). #316—8-hr photoperiod, note short flower stalk and short, broad-petioled leaves. #368—16-hr photoperiod, floral axis elongate, upright, spring-type leaves. #308—24-hr photoperiod, leaves long but prostrate (spring-type), traps intensely red. The short floral axis doubled its length before flowers opened.

2. *The 16-hour photoperiod.* Stabilization of leaf type slower in all regimes than under 24-hr light.

50-100 fc (Fig. 7D). Leaves thin, prostrate, papery, green; petioles long (9 cm), medium wide (1-1.5 cm) with wing tapering to base; traps small; floral axes attenuated, weak (Fig. 11, #576); only 5% of plants flowered while 28% produced initials. Deformities noted in stamens, pistiles and petals; only 2-3 flowers opened per inflorescence; no seed set.

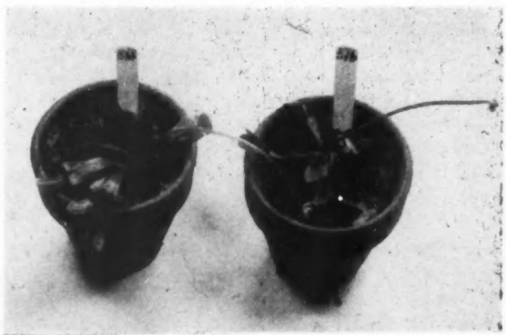

FIG. 11. Plants grown under low light intensity (50-100 fc). #568—8-hr day with leaves intermediate to final form (Fig. 7A), inflorescence did not mature. #576—16-hr day, leaves in early phase of heart-shape eventually produced; long, attenuated floral axis typical.

500 fc (Fig. 7E). Leaves in summer months generally erect, petioles long; traps medium size, somewhat leathery, glands red, intermediate tissues green giving traps pinkish tinge, darkening toward midrib (Fig. 10, #368) (Leaves similar to shaded, spring field leaves). During winter, leaves generally prostrate, no red color, petiole wings slightly wider; flower stalks long, well-developed, upright (Fig. 10, #368); 15% produced visible initials of which 50% flowered; viable seeds were set.

1000-1100 fc (Fig. 7F). Leaves identical with those of 24-hr regime, leathery, narrow—petioled (0.5 cm). (Fig. 12 shows several plants with varying leaf types, all except #374 eventually produced upright leaves). Leaves produced during winter months typical of spring field type—no red coloration and less leathery; flower stalks

and flower heads well developed, 40% of plants initiated and flowered, all set viable seed.

3. *The 8-hour photoperiod.* Leaf type fairly slow to stabilize and almost totall distinct from plants of other regimes.

50-100 fc (Fig. 7A). At first some leaves (Fig. 13) similar to those under higher light intensities of same day length but within 5 months, leaves typically long (6 cm), prostrate, dark green, thin and papery; traps small or represented by a "beak" of undifferentiated tissue at end of petiole. (Fig. 11, #568 leaves at intermediate stage in course of development). Flower stalks attenuated, 2% flowered although 10% produced visible initials; stamens and petals malformed, pistil poorly developed. No seed set.

500-fc (Fig. 7B). Leaves short (4-5 cm), leathery, intense dark green, prostrate with heart-shaped petioles and medium-sized traps (1.5 cm) (Fig. 14); no red color at any time. Floral axes short and thick, flowers well developed (Fig. 10, #316). All plants with visible initials (8%) developed flowers and viable seed.

1000-1100 fc (Fig. 7C). Leaves short, leathery, light green (glands slightly red), wide petioled (Fig. 15); traps (1.25 cm) shorter than under 500 fc; floral axes short, compact (Fig. 16); all plants with visible initials (13%) produced flowers and viable seed. Some of these 13% developed 2 or 3 different flowering axes during the summer, a phenomenon which is only occasionally observed in the field.

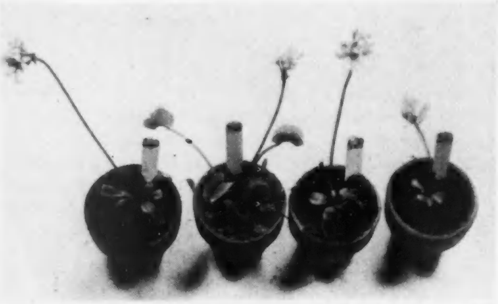

FIG. 12. Plants grown under high light intensity (1000-1100 fc) and 16-hr day. #542—typical summer type narrow-petioled leaves as eventually produced by all these plants; deep red traps of #374 typical but color develops gradually as leaves mature.

Transference of plants from one regime to another resulted in the production of leaf types characteristic of the new regime, the rate varying with the amount of change involved. Fastest response was always noted when the plants were put into the 24-hr regime (red color developed within 2 wks), probably because of the controlled temperature and humidity. However, floral initiation was never effected in uninitiated plants when transferred from one regime to another, whether from field or green-

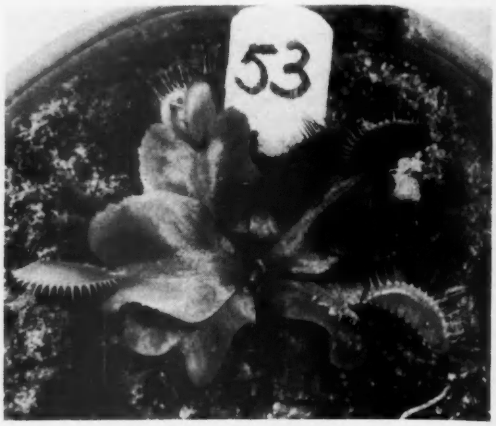

FIG. 13. Plant growth under low light intensity (50-100 fc) and 8-hr day. Typical of first leaves under low light, later traps are smaller and tissues less firm.

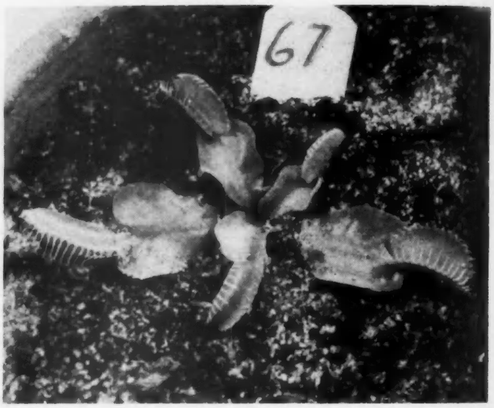

FIG. 14. Plant grown under medium light intensity (500 fc) and 8-hr day. Typical leaves are short, wide-petioled and no red color in traps which are relatively large.

FIG. 15. Plant grown under high light intensity (1000-1100 fc), 8-hr day. Leaves short, petioles relatively wide, color only at base of trap lobes.

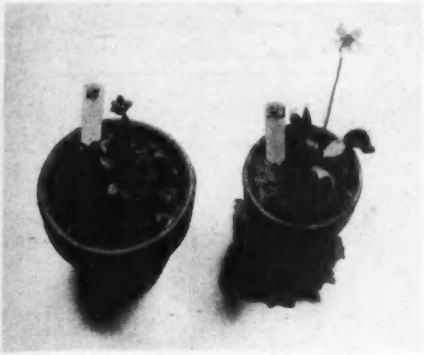

FIG. 16. Plant grown under high light intensity (1000-1100 fc). #15—8-hr day. Short, stout flower stalk, characteristic. #342—16-hr day. Traps deep red, leaves eventually all narrow-petioled, upright.

house (at a time when other plants in the group had visible initials) to controlled illumination or from one light condition to another. The controlled conditions provided did not result in floral initiation in any of these plants even after 13 months (second season) of exposure, regardless of their behaviour in the first season.

Several groups of plants were kept in cold storage (40°F) in both light (12 hrs) and total darkness for periods up to 3 wks, at different times of the year. Subsequent treatments were varied but again none was effective in producing visible development of floral initials.

It is realized that many of these treatments could have resulted in floral initiation, but subsequent development of these initials may have been arrested before they were macroscopically apparent. Also, many of the plants brought in from the field in January could have had floral primordia already present, and the increase in temperature in the greenhouse or the change of photoperiod could have been responsible for the early appearance of the initials.

Because it is well known that the carbohydrate-nitrogen ratio in some plants may control their flowering and fruiting (Kraus & Kraybill 1918, Hooker 1920) it is possible that an imbalance of carbohydrate-nitrogen in Dionaea might inhibit flower production, even after floral initials had been laid down. Shading with cheesecloth reduced the usual 40% field flowering substantially even though visible initials were present in normal numbers. In low light intensity daylength experiments the floral initials failed to develop. In both instances the plants could have been strongly carbohydrate deficient. Under open, natural conditions the soils never showed more than 2 ppm NH_4 and here a high or low supply of animal protein to the traps could likewise affect the balance and reduce the flowering percentages. In natural habitats, under normal illumination, too high a proportion of nitrogen produces rank growth and prevents development of floral axes. On the other hand, a nitrogen deficiency, compared with the amount of carbohydrate present, results in less vigorous growth, and, again, no flowering. On the basis of general observation it is more likely that plants in the field are mildly carbohydrate deficient than nitrogen deficient.

In the photoperiod experiments the yellow leaves under 24-hr high light intensity suggest nitrogen deficiency while under low light, the flaccid leaf type and floral initials that did not abort until almost mature suggest carbohydrate shortage (Fig. 11, #568).

Of the 42 plants which flowered in the greenhouse in 1955 only 10 flowered in 1956. This bears out what was found in the field, where only 40% of the plants marked as flowering in 1955, flowered again in 1956. However, by April 1957, none of the plants which had been in the greenhouse or laboratory since flowering in 1956, had produced visible flower buds.

These examples and the variability in time required for appearance of initials and flowers under different light intensities (Table 4) indicate that the requirements for floral development are extremely critical and effective only in a very narrow range. This being true, the low percentage of flowering of Dionaea in the field and in laboratory experiments is understandable.

Setting of seeds in Dionaea is somewhat differently related to light. Response to heavy shading in the field and to low light intensity with 8 and 16-hr days is similar to that of strawberry (Darrow 1927). Stamens, petals, and pistils of Dionaea are generally malformed. Thus, fruit formation is inhibited by floral deformities and no seeds are produced. Some plants, such as tomato, will flower under conditions of mild carbohydrate deficiency, but it is unlikely that this explanation applies to Dionaea because its plants, under heavy shade, do not show the rank vegetative growth usually associated with mild carbohydrate deficiency. Thus, although initially the carbohydrate and nitrogen content of some shaded plants may be appropriate for flowering, the shade conditions effectively prevent seed setting by causing malformation of both sexual and vegetative floral parts.

Although floral initials appear in field grown plants in early April, it is likely they are laid down much earlier, as is evidenced by their rapid appearance when field plants are brought into the greenhouse at earlier dates. Age of the plants is one factor which is involved in production of floral initials. Only mature Dionaea plants develop visible floral initials and this probably does not occur until they are more than 3 yrs old. Because the floral axis is terminal, its initiation prevents production of leaf initials until a new vegetative growing point is established. The new leaves which appear during floral development are obviously derived from leaf initials already present before floral primordia were laid down. The time lapse between the production of a leaf primordium and its appearance as a leaf initial is not known. Although floral primordia may

be laid down early and thus terminate new leaf production, observations were inadequate for generalizations. However, it was noted that in the number of individual plants, leaf production ceased for no apparent reason, to be renewed again after about a month. In these instances no floral initials appeared but this phenomenon could possibly be explained by assuming that during this time floral primordia were laid down but failed to develop. It is not known what combination of environmental factors is necessary to produce floral induction.

GERMINATION

Immediately after field-ripened seeds became available in the summer of 1955, germination tests showed them to be approximately 70% viable. Consequently, ripe seeds were stored at room temperature for further experiments in the fall. However, when tested again in September no germination occurred, and thus the problem of the length of viability arose.

The next spring, seeds were harvested as soon as they ripened in the greenhouse and the collections from different plants were stored separately. Experiments were then begun to test the germination percentage and the length of viability after different treatments and various storage periods by the following procedures:

1. Seed was considered ripe when exposed after the capsule had turned black and had ruptured. Some seed was collected immediately, and some was left on the plant for a definite length of time before collection.
2. After collection, the seeds were counted and stored in glass tubes at 72°F.
3. At predetermined intervals seed was set out to germinate on damp filter paper in covered petri plates. All temperatures were controlled at 72°F under a photoperiod of 12 hrs.
4. All seed was watered with distilled water. When the seeds had germinated and the seedlings were of sufficient size they were transferred to leached sand and watered with distilled water. It was from these that plants for the seedling nutrient experiment were taken.

Seed was set out to germinate at different time intervals after collection, at the rate of 10 seeds per test. Records were kept of the time of setting out and the time of germination, i.e., when the radical was first apparent. As the experiments progressed it became clear that there was no apparent after-ripening effect of the plant on the seed, once the capsule had opened.

After storage at 72°F for up to 4 weeks, half of each set of seeds was packaged in filter paper, layered in sand, and stored in the refrigerator (36°F) so that comparison could be made between cold storage and storage at normal temperatures.

Germination of unlayered seed averaged 87% for the first 40 days and 56% for the next 60 days (Table 5). After 100 days viability dropped to about 2% and after 140 days no germination occurred.

TABLE 5. Germination of unlayered seed.

No. of Replicates (sets of 10 seeds)	AVERAGE TIME (days)			% Germination
	Age (days)	To first seed	Between first and last seed	
8	0- 2	14	28	88
7	2- 4	18	58	89
15	5- 9	15	34	80
8	10- 14	12	22	87
6	15- 20	11	12	93
10	20- 29	14	18	83
5	30- 39	14	8	90
5	40- 49	10	19	66
8	60- 79	22	17	53
11	80- 99	23	8	50
11	100-139	19	..	2
15	140+	..	..	0

The time from setting out to the first germination of seed in a set varied somewhat, but over the whole time it averaged 16 days for unlayered seed and 11 days for layered. The time lag between the first seed germinating in a set and the last, also fluctuated, averaging 25 days for unlayered seed and 20 days for layered seed. As the unlayered seed aged, some increase in the average time lapse was noticed between setting out and germination, although this may be more apparent than real. (Table 6). No seed germinated when older than 126 days at the time of setting out, but some few seeds, which were set out within 2 weeks of ripening, were up to 145 days in age before they germinated. No unlayered seeds over this age were viable and viability at this age was extremely rare (Table 5).

TABLE 6. Germination of layered seed.

	DATE OF			AVER. TIME (days)		% Germination
	Collection	Layering	Setting out	First seed	Last seed	
Laboratory	April		July-Oct	11	23	97
	June	June 14	Nov-Mar	11	28	87
			July-Oct	11	39	82
Field	June	June 14	Nov-Mar	11	25	84

After layering, the percentage of germination remained high over the entire period of investigation. After 9 months, seeds were still showing 86% germination, equal to the average germination of up to 40 days for unlayered seed. The average over the whole 9 months period was 87%. Other differences have already been mentioned.

This difference in viability between layered and unlayered seeds is possibly explained by the presence of some metabolic mechanism within the seeds which is slowed down or completely stopped at low temperatures. Whether there is some production of autotoxins or other products in unlayered seed, is unknown. Water and alcohol extracts, made from inviable seed and evaporated down to dryness on the filter paper which was used to germinate viable seed,

had a slight retarding effect on germination, but the final percentages were equal to the controls.

Thus there is a mechanism within the seeds which ensures germination immediately after ripening at which time field-formed seed show approximately 70-75% germination (slightly lower than laboratory seed). After 40 days, germination is down to 66% and after 100 days it is negligible. Thus germination is insured in the field at that time of year when rainfall, humidity and temperature are high. Optimum temperature and light requirements for germination were not determined although it has been indicated that the seeds germinated equally well in darkness or light. No definitive tests were made to determine whether viability of unlayered seeds was increased by storage in darkness. High humidity is necessary for the survival of the seedlings after germination; seedlings show a marked intolerance even to short periods of low humidity, although with age this intolerance decreases somewhat. Thus the early germination in late summer, insures that the seedlings will be established in the field before winter sets in.

DISCUSSION

The laboratory experimental work to a large degree confirmed many of the generalizations and deductions drawn from observation in the field. It is well established that mature Dionaea plants survive desiccation over short or even extensive periods of time, either by reduction of leaf area and production of leathery tissues, or in severe conditions by going into dormancy. However, seedlings cannot become established in areas where soil drought is common.

Factors related to soil are certainly important in determining the occurrence of Dionaea. Presence of organic matter is favorable because it helps maintain a high moisture content. Clayey soils do not support Dionaea possibly because of too high a proportion of mineral nutrients, as suggested by nutrition studies, and perhaps also because of mechanical resistance as indicated by the absence or reduction of root growth in all experimental soils except sand or peat moss.

Light intensity, moisture supply and photoperiod all influence to some degree the shape and size of the leaves of Dionaea. Low light intensities result in broad-petioled leaves both in the field and the laboratory. However, moisture supply also influences width of petioles, for plants in full sunlight have broader petioles in moist habitats than in relatively dry sites. Whereas moisture and light intensity may each condition plants to produce specific leaf characteristics, length of day can modify these responses under experimental conditions. In general, under long photoperiods elongated leaves are produced and short photoperiods given short leaves. Thus, the seasonal changes in leaf morphology noted in the field are explainable for, in summer, all leaves tend to be long and with the short days of winter, all leaves tend to be short. Within this pattern, the leaves are widest wherever light intensity is reduced and wherever there is an excess of soil moisture at a given light intensity.

Insect material, digested and absorbed through the leaves, results in healthier, more vigorous plants than controls without the insects. The question of the need for insects is still unanswered but the feeding experiments indicated that high rates of insect feeding result in either a failure of the development of floral initials or failure of their production. These greenhouse experiments were done under light intensities much lower than in the field. It is possible therefore, that the rate of insect feeding was too high for the amount of photosynthesis occurring and that these plants may have had a carbohydrate deficiency. It may be that a very critical carbohydrate-nitrogen balance in Dionaea is necessary for complete development of floral initials. If this balance is easily upset the nonproduction of flowers in the experiments and under some field conditions is explainable.

Heavy shading affects the development of the flowers, resulting in abnormalities of stamens and pistils and possibly the pollen itself. Seed is not set under intensely shaded conditions in the laboratory if the flowers do come to maturity.

Germination experiments showed that the seeds, stored under normal conditions, have only a short period of viability although layering in sand under cold conditions will lengthen the time apparently indefinitely. The mechanism responsible for the short viability is not known.

DIONAEA MUSCIPULA IN ITS ENVIRONMENT

Dionaea muscipula is endemic to the coastal plain of the Carolinas and within this area is almost exclusively limited to the St. Johns' soil series. The general climate of the region does not appear to be a major factor in the delimitation of the boundary of the range. Dionaea has specific requirements which must be met before populations can be established. It is found mainly in restricted zones between true savannah and true pocosin but where this ecotonal area is very broad, as in semi-pocosin or semi-savannah, Dionaea may be found intermittently throughout. Depth of the ground water table, soil surface characteristics, nutrient level, light intensity and fire appear to be the most important factor in delimiting populations.

St. Johns' series soils have a high water table and an organic hardpan which is usually not more than 24 in. below the soil surface in Dionaea areas. The soil is acid with a pH range of 3.9-4.5. Although Dionaea will survive in less acid soils, growth above pH 6.5 is poor. With increasing distance from the pocosin edge the water table is further beneath the soil surface. This results in accelerated decay of organic matter, and therefore less accumulation of humus in the surface horizons. Near the pocosin, oxidation proceeds more slowly and a thin layer of incorporated organic matter accumulates at the surface. Thus in spring and summer, depth to which the soil will dry out is greater with increased distance

from the pocosin. Dionaea can survive but does not reproduce where water is seasonally out of range of the roots.

Dionaea is a light-demanding species but also requires a high water supply. Affecting the rate at which this plant is supplied with water is its root system, made up of 4-8 short, unbranched roots. Thus where the soil dries out below 2-3 in. in summer, roots cannot supply the plants with sufficient moisture. It is at such times that large plants with abundant starch reserve become dormant but small plants are killed.

At the pocosin edge, shrub vegetation is usually very dense and in such positions Dionaea may survive, but as flowering and seed setting do not occur under low light intensities, probably as a result of a critical carbohydrate-nitrogen requirement, satisfactory reproduction is not accomplished.

Seeds are ripe in June and July and field germination is first apparent at the end of July. The seed is viable only for a short length of time and in the field desiccation probably shortens it even more. Germination and development of the seedling occurs only in protected areas within the ecotone. High insolation and heavy rainfall which occur during the summer cause death of seedlings in unprotected sites by desiccation and battering. Therefore, the ability of seedlings to become established in an area is largely determined by the type of surface soil and the amount of protective vegetation.

Influencing the type of vegetation developed around a pocosin is fire. Where it is common, the ecotone has a relatively sparse ground cover made up of both savannah and pocosin species which are tolerant to differences in water supply. Where fire has not been a factor, dense ground cover is present. Only in areas of sparse vegetative cover will Dionaea be found in abundance and in a vigorous condition. Dionaea is fire tolerant. Growth and general vigor even appear to be stimulated by fire both by elimination of competition and by the effect on the plant itself.

Nutrient requirements are very low. The sandy coastal plain soils are very infertile and when Dionaea is transplanted into heavy soils containing abundant nutrients, growth is poor and death usually ensues. Part of the reaction of Dionaea to heavy soils may be due to its mechanical influence as root elongation is apparently impeded.

Therefore, it can be concluded that the boundaries of populations of Dionaea are determined by the amount of moisture available to the plant, and the light intensity of the area. Fire influences the latter factor. The total range appears to be determined by the gross soil characteristics such as acidity, nutrient content and texture. Whether Dionaea is extending its range or not is a moot point. The period of seed viability is very short and dispersal is slow, and both of these characteristics would tend to prevent rapid migration. However, it seems apparent that wherever conditions remain favorable for Dionaea in areas which it now occupies, populations are in no danger of annihilation.

SUMMARY

1. *Dionaea muscipula* was first reported from Brunswick, North Carolina by Governor Dobbs in 1759. John Bartram sent the first dried material to England where it was examined and described by Ellis in a letter to Linnaeus in 1769 (published 1770) after he had seen living material brought over by William Young in 1768.

2. The numerous early investigators were primarily concerned with the nature of leaf structure and action. The relation of the plant to its environment, and its ranges in tolerances were almost completely neglected.

3. The maximum substantiated range of Dionaea extends from Chocowinity, Beaufort County, North Carolina, south to the Santee River, South Carolina and westward to the Moore County sandhills area. Although apparently not "doomed to extinction," human interference limits its occurrence in some areas.

4. Inference from the geological history of the coastal plain suggests that the possible center of dispersal of the present distribution was the Moore County sandhills area from populations postulated to have been present there in pre-Pleistocene times. It is suggested that water has been the main dispersing agent.

5. General climate within the range is not significantly different from that 50 mi. outside, and is not considered a major influence in the delimitation of the boundary.

6. Topography of the coastal plain is level, and as a result, one of the main influencing factors on the development of soils from the sandy parent materials has been the height of the water table. Dionaea is almost exclusively confined to the St. Johns' soil series which is predominantly sand, has a high water table, an organic hardpan, a thin surface layer of black incorporated organic matter, is acid in reaction and very infertile.

7. Pocosins and savannahs are two morphologically distinct vegetation types of the coastal plain, developed primarily as a result of slight differences in elevation and hence differences in the depth of the water table which affects the soil type. A gradient in vegetation and soil profile exists between them and in this ecotonal position Dionaea is normally found.

8. Dionaea is a light-demanding species but also requires a high water supply. Thus the savannah boundary of the Dionaea population is established by the depth to which the surface soil dries for this in turn influences the amount of organic matter present in the surface soil and the water supply in summer. The pocosin boundary is established by the density of overhanging vegetation.

9. Flowering and seed setting do not occur under low light intensities. Although Dionaea is able to survive under heavy shade, satisfactory reproduction

does not occur. It is probable that Dionaeas has a high minimum light requirement for photosynthesis and that its flowering depends upon a very critical carbohydrate-nitrogen balance.

10. Fire is a very important factor influencing the density of vegetation in the savannah-pocosin ecotone. Without this factor heavy ground vegetation is developed which would eventually eliminate Dionaea populations.

11. As for external morphology, Dionaea has a bulbous rhizome formed from overlapping leaf bases containing high starch reserves. The flowering axis is terminal, necessitating a new adventitious bud for continued vegetative growth. The root system is made up of a few short unbranched roots possessing long, persistent root hairs. The leaves arise from one end of the rhizome and appear as a rosette. Two main types of leaves are formed: winter-type—short, broad petioled and prostrate and summer-type—long, narrow-petioled and upright. Spring leaves are intermediate. Leaves produced under shade show a variation of form—are thinner in texture and always broad-petioled.

12. Photoperiod is the main factor influencing leaf length, and light intensity the main factor influencing petiole width. Thus under short photoperiods short leaves are produced and under long photoperiods, long leaves. A decrease in light intensity brings about an increase in petiole width. Under a given light intensity excess soil moisture may increase petiole width slightly.

13. Dionaea is fire resistant and after burning is usually one of the first plants to show renewed growth apparently because the sheathing leaf bases protect the growing point. Other surface-rooted plants are destroyed by frequent fires while Dionaea appears to be invigorated. If the growing point is injured, adventitious budding from the leaf bases will occur in well-developed plants.

14. No associated species can be designated with confidence as Dionaea indicators, since they vary from one site to another, are mostly tolerant of a wide moisture range and are typical of either savannah or pocosin.

15. Well-developed Dionaea plants survive prolonged periods of drought by going into dormancy. Drought conditions may result in two cycles of growth following total dormancy in a single summer. Well-developed Dionaea will also survive prolonged periods of submergence under water. Neither submerged or drought-dormant plants produce flowers and seedlings will not survive under either condition.

16. Germination of fresh seed takes place within 10-21 days after placing in the germinator while after 100 days storage, germination is negligible unless the seed is layered in cold storage. Thus, field germination necessarily occurs in summer (July and August) because viable seed are not available in spring. Therefore, the significance of suitable soil surface (light humus on the sand) and protective vegetation is understood, as the physical environmental conditions would otherwise prevent seedling establishment. Development of seedlings is slow—after 12 months the diameter of the leaf rosette rarely exceeds 2 cm.

17. No criteria could be determined for estimating the age of these plants. Differences in leaf type and structure are apparent between young and adult plants. Mature plants are those considered to be capable of producing flowers and having large well-developed rhizomes. Flowering of seed-grown plants probably does not occur for at least 3 yrs. Flowering of plants from adventitious buds, developed on mature vegetative tissues, may occur within 12 months.

18. It is concluded on the basis of this investigation that the total range of Dionaea is probably determined by the soil type. Boundaries of local populations appear to be determined by the depth to which the surface soil dries out in dry periods and the light intensity. Seed viability, dissemination, and germination requirements determine the extent to which the plant can colonize new areas. Within well-established populations the frequency of fire chiefly determines the vigor and survival of the plants. Apparently the total range is stable at present and existent populations should survive except in areas where human activities alter the basic requirements of a suitable habitat.

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